

POST-FIRE RESTORATION TREATMENT EFFECTS ON THE SOIL SEED BANK OF A PINYON-
JUNIPER WOODLAND IN ZION NATIONAL PARK, UTAH, USA.

By Hondo Brisbin

A Thesis

Submitted in Partial Fulfillment
of the Requirements for the Degree of
Master of Science
in Forestry

Northern Arizona University

August 2010

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ABSTRACT

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Invasive annual bromes threaten native diversity across vast areas in much of the western United States. A variety of techniques have been employed in an attempt to control these plants, yet populations continue to persist and expand. Recently however, a measure of success had been achieved, at least in the short-term, through use of the herbicide, imazapic (Plateau®). This study sampled the soil seed bank to help monitor the effectiveness of treatments utilizing imazapic and a native seed mix to control *Bromus* species and enhance perennial, native plant establishment following a wildfire in Zion National Park. One year post-treatment, *Bromus* was significantly reduced in plots sprayed with herbicide. By the second year post-treatment, the effects of imazapic were less evident and convergence with the controls was beginning to occur. Emergence of seeded species was low for the duration of the study. Dry conditions and possible interactions with imazapic probably contributed to the lack of seeded native species emergence. *Sporobolus cryptandrus* (sand dropseed) performed the best out of all the seeded native species.

We also examined how the treatments affected the soil seed bank community as a whole and compiled general, descriptive data as concerning the composition of the soil seed bank. We found evidence that the herbicide was reducing several native, annual forbs and one nonnative, annual forb. However, overall effects on the community were not significant. Annual species comprised the majority of seedlings emerging from soil samples. Over the course of the study, 40 species were identified representing 25 different families. The majority of seedlings were forb species followed by grasses and then shrubs. All but six of the species were native.

The results of our study were similar to what others have found in that imazapic is effective in providing a short-term restoration window in areas invaded by *Bromus* species but, can also impact emergence of non-target, native species. To help mitigate possible negative interactions with seeded native species, we recommended incorporating a time-lag between herbicide and seed application. We also caution against using imazapic on sites that are not highly invaded in order to prevent unintentional damage to the native plant community.

ACKNOWLEDGEMENTS

I thank my chair, Andrea Thode, and committee members, Margaret Moore and Molly Hunter, for all their help, support and patience throughout this project. I thank Matt Brooks and staff at the US Geological Survey, Western Ecological Research Center for aiding in project design and implementation. I also thank the wonderful people at Zion National Park including, Cheryl Decker, Kristen Legg and Katie Johnson, for their support and arrangement of so many logistical matters. I thank staff members of the School of Forestry and the Ecological Restoration Institute, especially Judy Springer and David Huffman, for answering and helping me with so many questions. I thank Brian Brost and Daniel Laughlin for their generous donation of time and effort in imparting to me a fraction of their eloquent knowledge of the cryptic world of community-based statistical analysis. My heartfelt thanks go out to the tried and true technicians who so admirably assisted me in the field and spent countless hours laboring away in the greenhouse. They are: Matt Flying, Ryan Mesaros, Jerry Elan and Mark Lawler. I also thank Phil Patterson and Brad Blake for the help, graciousness and humor that were so prevalent during my long tenure in the NAU greenhouse facility. Finally, I thank my friends, colleagues and family for all of their kind words, love and constant encouragement. This project was funded by the Joint Science Fire Program (07-2-4-0) and the US Geological Survey, Western Ecological Research Center.

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PREFACE

This thesis is written in manuscript format with the literature cited placed at the end of each chapter. Chapter 3 is based off of an analysis of data obtained through methods described in Chapter 2. Therefore, replicate tables and figures were not included in Chapter 3. Chapter 2 and Chapter 3 will be combined and submitted to Weed Technology for peer review.

CHAPTER 1

Introduction

Soil seed banks represent the spatial accumulation of seeds within the soil profile and on the soil surface (Paintner 1990). In semiarid environments, the majority of seeds occupy the litter layer and the top 2-3 cm of the soil (Nelson and Chew 1977; Koniak and Everett 1982). Seed banks vary spatially and temporally with inputs arriving and departing throughout the year and seed accumulation occurring at different points of the soil profile and at different locations on the landscape (Coffin and Lauenroth 1989; Simpson et al. 1989). Species composition fluctuates depending upon location and season, but is usually comprised of numerous annual and biennial species and few perennials. Annual species can make up to 80-90% of the community (Allen et al. 2008). Inputs from the soil seed bank can greatly influence the aboveground plant community following disturbance. Stages of early succession often see high correspondence in aboveground and belowground composition (Olmsted and Curtis 1947). This similarity tends to decline as succession proceeds and the surface vegetation becomes dominated by perennial species (Chippindale and Milton 1934; Paintner 1990; Abella et al. 2007).

The incidence of fire can have a detrimental effect on soil seed banks due the tendency for seeds to be congregated in the flammable litter and organic layers. However, seeds residing just below the surface often survive due to the insulating properties of mineral soil and the seed coat (Keddy et al. 1989). Other seeds respond to fire and will germinate following some interaction of cues such as heat shock, smoke, charred wood, light and temperature (Auld and Denham 2006). Seeds that do persist or

move in from outside sources can have a large influence on the immediate post-fire community. This fact is perturbing in light of the current preponderance of annual, invasive species in the West and the likelihood of increased, high severity fire in responses to climate change and years of fire exclusion (Humphrey and Schupp 2002; Floyd et al. 2004; Brown et al. 2008). *Bromus tectorum* (cheatgrass) is a particularly aggressive and invasive, nonnative, annual grass that now occupies millions of hectares in the western region of the United States. A soil seed bank study in Utah, found little evidence of its presence within the understory community of the study area. The seed pool however, contained large amounts of *B. tectorum* seed even under unburned, late-seral vegetation. A subsequent fire removed much of this seed, but what remained was sufficient to double pre-fire populations one year after the fire. Inputs from native seeds into the aboveground assemblage were minimal (Hassan and West 1986).

The accelerated threat of invasive species in the West has necessitated the need for integrated approaches to post-fire restoration (Humphrey and Schupp 2002; Brown et al. 2008). Efforts to replenish seed banks with seeding alone often fail due in large part to competition from nonnative species (Brooks 2005; Davison and Smith 2007). Previous methods for mitigating the threat of exotics prior to seeding have had mixed results, but are often not sufficient, especially when trying to control prevalent species like *B. tectorum* (Stewart and Hull 1949; Canode et al. 1962; Evans et al. 1970). Historical conditions allowed for the introduction and proliferation of *B. tectorum* and other annual bromes, but there are other factors that have enabled them to maintain a dominant position in many plant communities.

Bromus rubens (red brome) and *B. tectorum* for instance, are admirably suited to preempt resource allocation. They proliferate by producing large quantities of seed which germinate in the fall, or in the following spring. Germination typically occurs well in advance of most native species allowing it to deplete soil moisture which can be extremely limiting in semi-arid environments (Melgoza et al. 1990; Floyd et al 2006; Smith et al. 2008). Seedling emergence can occur under a variety of soil temperatures and fall-germinated plants, although undergoing dormancy during the winter, continue to experience root growth thus giving individuals a significant advantage the following spring (Thill 1979; Mack and Pike 1983; Beckstead et al 2007; Meyer et al 2007).

Additionally, areas dominated by these invaders can be kept in a relatively constant state of disturbance due to regular instances of drought, wind and fire. Aboveground biomass dries early in the growing season, thus introducing an ample layer of fine fuels. This often results in drastically reduced fire-return intervals, which exerts further stress on native, perennial plants (Stewart and Hull 1949; Brooks et al. 2004; Meyer et al. 2007). The high germination rate, high seed production and seed bank carryover of annual bromes emphasizes the value of incorporating soil seed bank assays into monitoring programs. Quantification of seed reserves can provide useful information for designing and implementing control measures and for monitoring purposes after treatments have been applied (Smith et al. 2008). For instance, discovery of substantial amounts of seed in the soil seed bank can lead to a decision to utilize a pre-emergent herbicide such as imazapic (Plateau®)

In recent years, greenhouse and field trials have had reported success when using imazapic to controlling nonnative, annual species (Monaco et al. 2005; Vollmer and Vollmer 2006; Davison and Smith 2007; Baker et al. 2009; Morris et al. 2009). Imazapic targets fast growing tissues which makes it ideal for controlling *B. tectorum* based on its tendency to start actively growing prior to most native species. It also binds with the soil and remains active until metabolized by plants, degraded by soil microbes or leaching occurs due to elevated precipitation (Tu et al. 2001; O'Neil 2008). Previous studies have indicated that low rates of imazapic applied in the fall are most effective at reducing *B. tectorum* while minimizing negative impacts on native plants (Shinn and Thill 2002, 2004; Kyser et al. 2007; Baker et al. 2009). There is evidence however, that imazapic does adversely affect seedling development of some native species, especially in moisture depauperate, post-fire environments (Bekedam 2005). Many questions still exist in respect to imazapic effects in the context of landscape-scale restoration projects.

Currently, Zion National Park is in the forefront of research focused on native plant restoration, *Bromus* species control and imazapic use. A study in Zion Canyon looked at various combinations of prescribed fire, mowing, imazapic application and native seed and their effect on exotic brome species and native establishment. Fall burns plus imazapic application was most effective at impacting the bromes, but herbicide sprayed in the spring following the burn produced the highest densities of native species (Matchett et al. 2009). Evidence suggested that native species were inadvertently controlled when the herbicide was applied pre-emergent, but less of an

effect was recorded with post-emergence application (Matchett et al. 2009). A nursery study applied different rates of imazapic in the presence and absence of brome mulch. A moderate rate (0.59L/ha) reduced brome species and had less of an impact on native emergence, but was ineffective when mulch was present (Dela Cruz 2008). This indicated the possibility of using this rate in post-fire environments where mulch would be largely absent.

An opportunity arose in the summer of 2006 when a large wildfire (Kolob Fire) burned some 4,000 hectares in the southwestern corner of Zion National Park. Pockets of *B. tectorum* and *B. rubens* were known to exist at this site prior to the fire and large populations were growing on adjacent non-parklands. A prescription was designed that called for spraying Imazapic at the desired 0.59L/ha and also included the application of a native seed mix. Study plots were installed to monitor aboveground and belowground treatment effects. Both brome species are capable of inundating the transient seed bank (seeds germinate in the same season as seed shatter) and the persistent seed bank (seeds overwinter to germinate the following spring or fall) (Smith et al. 2008). This study analyzed the soil seed bank to aid the Park in assessing post-treatment changes in *Bromus* densities, native plant establishment rates and overall effects of the treatments on the soil seed bank community.

In Chapter 2, I analyze data collected in 2006, 2007 and 2008 to assess the efficacy of imazapic and the native seed mix in reducing populations of *Bromus* species and assisting in the reestablishment of native species. Little is known about the interactions of imazapic and native species commonly used in post-fire seeding

operations and very few studies have monitored the effects of imazapic and native seeding from the standpoint of the soil seed bank.

In Chapter 3, I analyze the same data utilized in Chapter 2, but exclude *Bromus* species in order to focus solely upon treatment effects on the rest of the soil seed bank community. My goal is to determine if any non-target, native species are being adversely affected by the herbicide and if so, to ascertain whether or not control of *Bromus* species appears to outweigh inadvertent damage to the native community. In Chapter 4, I present a short discourse on implications for management based upon my findings.

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CHAPTER 2

Soil Seed Banks as a Metric for Determining Post-Fire Restoration Success in Annual, Nonnative *Bromus* Invaded Environments

Abstract

Invasive annual bromes threaten native diversity across vast areas in much of the western United States. A variety of techniques have been employed in an attempt to control these plants, yet populations continue to persist and expand. Recently, a measure of success had been achieved, at least in the short-term, through use of the herbicide imazapic. This study sampled the soil seed bank to help monitor the ability of imazapic and a native seed application to reduce *Bromus* occurrence and promote native species reestablishment following a wildfire in Zion National Park. One year post-treatment, the *Bromus* seed bank was significantly reduced in plots sprayed with herbicide. By the second year post-treatment, convergence with the controls was beginning to occur and only plots treated with a combination of herbicide and seeded species maintained significantly lower counts of *Bromus*. Germination of seeded species was low in both years of the study and emergence was driven by the perennial grass, *Sporobolus cryptandrus*. Our study found imazapic maintained an acceptable level of *Bromus* control for one year following application, but potentially had an adverse effect on emergence of some of the native seeded species. Incorporating a time-lag between herbicide and seed mix application could increase seeded species performance.

Introduction

Bromus tectorum (cheatgrass), *Bromus rubens* (red brome) and other annual brome species now occupy vast areas in much of the Intermountain West (Whisenant 1990; Monsen 1994; Belnap et al. 2003). A variety of factors facilitated the spread of annual bromes including disturbance attributed to historical pastoral and agriculture practices and the general inability of native vegetation to withstand *Bromus* competition (Mack 1981; Young et al. 1987). Areas dominated by these invaders can be kept in a relatively constant state of disturbance due to regular instances of drought, wind and fire. In particular, *B. tectorum* dries early in the growing season, thus introducing an ample layer of fine fuels. This often results in drastically reduced fire-return intervals, which exerts further stress on native, perennial plants (Stewart and Hull 1949; Brooks et al. 2004; Meyer et al. 2007). Although fire reduces *B. tectorum* seed reserves in both the aerial and upper portion of the soil seed bank, surviving seed and inputs from adjacent sources allows for a return to pre-fire densities within a few years (Monaco et al. 2003; Brooks 2005; Brown et al. 2008).

Beyond facilitating fire, *B. tectorum* is suited to preempt resource allocation. As an annual grass, it proliferates by producing large quantities of seed that can readily germinate in the fall, or in the following spring. Whichever the case, germination occurs well in advance of most native species allowing it to deplete soil moisture (Floyd et al. 2006; Smith et al. 2008) which can be extremely limiting in semi-arid environments. The actual method by which this species is able to take advantage of such a situation is

evident in the ecology of its seeds. *B. tectorum* seeds exhibit physiological dormancy at the time of seed dispersal (early summer) and requires an after-ripening phase of warm, dry weeks before germination is possible. Moisture arriving at this point can result in complete germination of viable seed (Chepil 1946; Steinbauer and Grigsby 1957; Hulber 1955; Meyer et al. 2007). Though this response is typical in mesic regions, drier areas often do not produce sufficient precipitation to replicate this scenario (Mack and Pike 1983). Seeds that do not germinate in the fall, and are not killed by extreme temperatures, often produce cotyledons the following spring or they may undergo a secondary dormancy and germinate the next fall (Mack and Pike 1983; Beckstead et al. 2007; Meyer et al. 2007).

Previous efforts aimed at controlling *B. tectorum* have focused on removing emerged plants prior to seed development. These efforts include grazing, chemical application, plowing and prescribed fire (Canode et al. 1962; Evans et al. 1970; Bunting et al. 1987; Emmerich et al. 1993; Whitson and Koch 1998).

Of these methods employed to control *B. tectorum*, only deep plowing and prescribed fire have had much effect on seeds in the soil seed bank. In both cases however, there still remains unaffected seed and both methods can adversely affect native species (Stewart and Hull 1949; Evans et al. 1970). The fact that soil seed bank carryover is common in arid to semi-arid regions, emphasizes the need for control measures that target pre-emergent populations (Smith et al. 2008).

In recent years, greenhouse and field trials have had relative success using imazapic (Plateau®) herbicide (Vollmer and Vollmer 2006; Davison and Smith 2007; Baker et al. 2009; Morris et al. 2009). Imazapic targets fast growing tissues which makes it ideal for controlling *B. tectorum* based on its tendency to actively start growing prior to most native species. It also binds with the soil and remains until degraded by soil microbes or leaching occurs due to elevated precipitation. This process can be as short as a month or take up to two years depending upon environmental conditions (Tu et al. 2001; O'Neil 2008). Previous studies have indicated that low rates of imazapic applied in the fall are most effective at reducing *B. tectorum* while minimizing negative impacts on native plants (Shinn and Thill 2002, 2004; Kyser et al. 2007; Baker et al. 2009). There is evidence however, that imazapic does adversely affect seedling development of some native species, especially in moisture depauperate, post-fire environments (Bekedam 2005).

Many questions still exist with respect to imazapic effects in the context of landscape-scale restoration projects. Currently, Zion National Park is in the forefront of research focused on native plant restoration, *Bromus* control, and imazapic use. A small-scale study in Zion Canyon looked at various combinations of prescribed fire, mowing, imazapic application and native seed and their effect on exotic brome species and native plant establishment. Fall burns plus imazapic application was most effective at impacting the bromes, but herbicide sprayed in the spring following the burn produced the highest densities of native species (Matchett et al. 2009). Evidence suggested that native species were inadvertently controlled when the herbicide was applied pre-

emergent, but less of an effect was recorded with post-emergence application (Matchett et al. 2009). In a nursery study, different rates of imazapic were applied in the presence and absence of brome mulch. A moderate rate (0.59L/ha) reduced brome species and had less of an impact on native emergence, but was ineffective when mulch was present (Dela Cruz 2008). This indicated the possibility of using this rate in post-fire environments where mulch would be largely absent.

An opportunity arose in the summer of 2006 when a large wildfire (Kolob Fire) burned some 4,000 hectares in the southwestern corner of Zion National Park. Pockets of *B. tectorum* and *B. rubens* were known to exist at this site prior to the fire and large populations were growing on adjacent non-parklands. Park staff and a BAER (Burned Area Emergency Response) team designed a prescription that called for spraying Imazapic at the desired 0.59L/ha and also included the application of a native seed mix. Study plots were installed to monitor aboveground and belowground treatment effects. Both brome species are capable of inundating the transient seed bank (seeds germinate in the same season as seed shatter) and the persistent seed bank (seeds overwinter to germinate the following spring or fall) (Smith et al. 2008). Therefore, it was believed that quantification of seed reserves would further aid efforts to encapsulate overall changes in *Bromus* populations and in predicting potential annual emergence. This study analyzed the soil seed bank to aid the Park in assessing post-treatment changes in *Bromus* densities and native plant establishment rates.

The primary objective of this study was to gauge the effectiveness of the imazapic treatment on reducing *Bromus* in the soil seed bank. We hypothesized that 1) compared to the control plots, emergence would be significantly less in the herbicide-only plots, but due to excessive competition, seeded native species establishment would not be sufficient in the seeded-only plots to have any appreciable effect on reducing *Bromus* occurrence, 2) plots treated with a combination of herbicide and seed would yield the lowest counts of *Bromus* and have the highest rates of seeded native species establishment and 3) imazapic would most effectively diminish seed resources one year following application, when the herbicide should be most active, and begin to converge with the controls by the second year. A secondary objective was to assess the performance of the native seeded species. We hypothesized that *Sporobolus cryptandrus* (sand dropseed), in the presence of herbicide or not, would have the best establishment rate due to its active seed production and highly germinable seed.

Methods

Site Description

This study was conducted within the Kolob burn, which started in June 2006 near the southwestern corner of Zion National Park in southern Utah (37°9.38' N, 113°29.35'W) (Figure 2.1). The fire burned 4,256 hectares, the majority (75%) being in pinyon-juniper woodland, the remainder in shrub/grassland and ponderosa pine. Based on the thirty-year average, the average annual temperature for this region is 16° C with 37 days over 38° C and 74 days below 0° C. There are 62 days of measurable precipitation per year, four of which are snow. Annual precipitation averages 38 cm, the

majority of which falls during the winter (October-April) and averages 25 cm (Western Regional Climate Center 2005). During the study period, annual precipitation was slightly below average in all years of the study. The first two years (2006 & 2007) exhibited similar patterns with most moisture arriving in October of the previous year and late spring/early summer (although, more precipitation fell in the monsoonal months of July and August during 2007). Winter moisture (December, January, and February) was the major contributor in 2008 with far less precipitation falling during the late summer monsoons than occurred in 2006 or 2007 (Fig 2.2).

Two study sites were selected; one in pinyon-juniper and one in a shrub-grassland area. The pinyon-juniper site is dominated by *Pinus monophylla* (singleleaf pinyon) and *Juniperus osteosperma* (Utah juniper). Understory species include *Artemisia tridentata* (big sagebrush), *Amelanchier utahensis* (Utah serviceberry) and *Purshia mexicana* (cliffrose). Soils are well drained and consist of very cobbly loam within the top 5 cm and gravelly clay loam from 5-12.5 cm. Dominant species in the shrub/grassland site are *Gutierrezia sarothrae* (broom snakeweed), *Lycium andersonii* (wolfberry), *Convolvulus arvensis* (field bindweed) and *Pleuraphis jamesii* (galleta grass). Soils consist of fine, sandy loam. Parent material for both study sites consists of eolian deposits derived from shale and sandstone over residuum weathered from basalt. Slopes range from 2-20 percent.

Imazapic was applied via helicopter to 3,577 ha at the recommended rate of 0.59L/ha. This occurred in late October of 2006. The majority of the burned area was thought to be relatively free of *Bromus* before the Kolob fire occurred. Therefore, it was

believed that the herbicide would be sufficient to prevent colonization and that native propagule densities would be adequate for natural revegetation. The situation in the northwestern corner of the study site was different. This area was known to be occupied by both *B. tectorum* and *B. rubens*, for at least several decades. Seed reserves of native species were likely scarce given the long-term presence of these exotics and their ability to monopolize the soil seed bank. To assist native succession, this region received an additional aerial application (9.1 kg/ha) of a native seed mix comprised of *Sporobolus cryptandrus*, *Elymus elymoides* (bottlebrush squirreltail), *Penstemon palmeri* (Palmer penstemon) and *Sphaeralcea ambigua* (desert mallow) (Table 2.2). Seeds were applied several days after the herbicide application. All species are perennial, had a pre-fire presence and have some ability to compete with *Bromus* (Humphrey and Schupp 2002; Leger 2008).

This project was designed to assess treatment effects within the soil seed bank. It added to a co-occurring study established to monitor the effects of the treatments on the aboveground vegetation (Thode et al. 2010). Initial site selection was based upon stratification of the burned area by treatment type, vegetation type and geological groupings with the goal of reducing onsite environmental variability. All sites were located in areas of high fire severity as these areas were targeted for post-fire treatments.

Study Site Design

Pinyon-Juniper Site

The pinyon-juniper site contained a total of 48 plots. A randomized complete block design was implemented with each block containing four plots for a total of 12 blocks. Plots are 5 x 30 m and contain one of the following randomly assigned treatments: control, seeded, herbicide, seeded and herbicide (Figure 2.3). A 15-m buffer was established around each plot to aid in accurate aerial application of the herbicide. Individual plots were separated by at least 30 m and no buffers were closer than 15 m to any road. Seeded plots were hand-seeded at a rate consistent with the aerial application to insure precision.

Shrub-grassland Site

The shrub-grassland site was treated with herbicide only and thus a paired design with untreated control and herbicide-treated plots was used (Figure 2.4). Plot implementation time was limited so smaller plots were established (2 x 2 m) to facilitate rapid installment (Figure 2.4). Buffers were set at 2 m in each direction and a minimum of 4 m between plots. Polyethylene plastic sheeting (6 mm) was placed over each control prior to herbicide spraying in order to maintain plot integrity. The sheeting was removed within 24 hours of application.

Seed Bank Sampling

Seed bank collection was done in late October-early November when soil seed reserves were most replete with available annual and perennial species. Collections were made just prior to treatment application in the fall of 2006 and again in the fall of

2007 and 2008. At the pinyon-juniper site, samples were obtained at 5-m intervals (5, 10, 15, 20, 25) along the west and east side of each vegetation plot. A sample consisted of a composite of two smaller sub-samples taken from around the perimeter of a 1-m quadrat (Figure 2.3). At the shrub-grassland site, samples were composited from soil taken from just outside each 2 m plot (Figure 2.4). To help overcome the spatial anomalies inherent in belowground seed distribution, collection of numerous, small samples was preferred to taking only a few large samples (Bossuyt et al 2007). However, the tendency of seeds to be clumped around a parent plant can still lead to an underestimation of species composition when samples fall within seed scarce regions between plants (Bigwood and Inouye 1988). Due to inconsistencies in the aerial application of the herbicide treatment, some subsamples at the pinyon-juniper site were compromised and not used in the analysis (Table 2.3).

Initial samples were collected by pressing a tin soil canister (height 4.4 cm, diameter 6.0 cm) into the ground to a depth of 3.0 cm (85 ml sample). A metal spatula was then inserted underneath the canister to aid in the removal of a complete sample. Sampling was restricted to the top 3 cm of the soil as previous studies have found few seeds present below 2-3 cm in desert soils (Price and Reichman 1987; Ferrandis et al 2001; Kemp 1989). Obstructions such as rocks and woody debris (exceeding 1 inch in diameter) were picked up (with any external soil being brushed into the canister) and placed to the side. Standing vegetation was also avoided. Samples were then placed into a labeled bag and transported back to Flagstaff, AZ where they were placed outside in sealed, plastic containers for 2-3 months in order to vernalize the seeds. Outside

conditions ranged from below freezing to 5° C. Samples were later brought into the greenhouse to be processed for the seed bank emergence portion of the study. The greenhouse was not kept at a constant temperature. Temperatures ranged from a low of 5° C to a high of 20° C during the winter months and 10° C to 30° C in the summer. No artificial lights were used.

Seed Bank Determination

The contents of the seed bank were ascertained using the emergence method standardized by the US Geological Survey, Western Ecological Research Center. These protocols are based on earlier methods used in the Great Basin (Young et al. 1969; Evans and Young 1975; Young and Evans 1981), but were modified to capture annual plants found in the Mojave Desert (T. Esque et al. unpublished data). Many of these same annuals proliferate at our sites as well. Soils were brought out of storage, air-dried and ran through a 2 mm mesh sieve. Stones and organic debris were discarded after first removing any adhering soil. A one-half cup of the sifted sample was then mixed with one-half cup of Vermiculite to increase water retention. Each mix was placed in a 6 inch bulb pot lined with synthetic weedblock fabric. Pots were randomly placed on greenhouse benches and watered. Seedlings were identified, tallied and plucked as they emerged. Given that distinguishing between *B. tectorum* and *B. rubens* can be difficult at the seedling stage, they were collectively identified as *Bromus*. This process continued until germination had mostly ceased (4-6 weeks). The soil mixtures were allowed to dry out for 2-3 weeks followed by a second watering phase (3-4 weeks). This pattern was repeated two more times with potassium nitrate (50 ml per pot/0.01 M

solution) being added at the beginning of the third phase (2-3 weeks) and Gibberellic acid (50 ml per pot/ 6.5×10^{-4} M solution) added at the beginning of the fourth phase (2-3 weeks). The dry-down period approximates natural moisture fluctuations necessary for germination to occur in some desert species (Baskin and Baskin 1998; Meyer et al. 2007). The chemical additives were included due to their previously documented ability to stimulate germination in perennial species (Jones and Nielson 1992; Bell et al. 1995; Baskin and Baskin 1998). Nomenclature for all emerging species followed USDA, NRCS (2009).

The number of seeds/m², were approximated by first determining the surface area of a soil canister (28.3 cm²). This number was multiplied by the total number of subsamples in a plot to determine the total surface area sampled. The area of one square meter was then divided by the total surface area sampled. The number of seeds emerging from each sample was multiplied by this result in order to estimate the number of seeds/m² (the multiplier varied by plot depending upon the amount of samples compromised during treatment application) (Warr et al. 1994). Finally, trial pots were set up in the greenhouse to test the viability of the seeded native species. Twenty seeds of each species were randomly selected from a seed sack and placed into individual bulb pots containing potting soil. Seedlings emerged from the majority of seeds for all species.

Data Analysis

All analysis was performed using PC-ORD software (5.31). Permutational multivariate analysis of variance (PerMANOVA) was used to detect differences in

Bromus emergence across the four treatments at each site in each year of the study (Euclidean distance, 4,999 permutations). This analysis of variance technique generates an F-statistic using permutations of the observations, thus allowing for the inclusion of non-normal data and multiple distance measures (Anderson 2001). Detection of a significant treatment effect ($\alpha = 0.05$), was followed by post-hoc pair-wise comparisons that allowed for a more detailed treatment analysis. PC-ORD does not correct the p values for multiple comparisons. Without a correction, the chance of committing a Type I error was increased to about 20%. However, use of the prescribed Bonferroni correction dramatically increased the probability of committing a Type II error. Based off of personal correspondence with a statistician and current literature, we opted not to use the correction (Anderson 2001; Nakagawa 2004). PerMANOVA was also used to test for significant pockets of *Bromus* prior to treatment application. A randomized complete block design was used in the field to reduce error from confounding environmental factors.

Results

Effects of Imazapic at the Pinyon-Juniper Site

Emergence of *Bromus* seedlings was low in the soil samples prior to treatment application (Table 2.4). A PerMANOVA analysis revealed no significant difference in average number of emerged *Bromus* seedlings among any treatment plots indicating a relatively even distribution of seeds across the study ($df = 47$, $f = 0.619$, $p = 0.706$). A significant treatment effect was evident in the first year following treatment application ($df = 47$, $f = 7.454$, $p = 0.0008$). Consistent with our first hypothesis, average seedling

emergence was significantly lower in herbicide-only plots, but not in seeded-only plots, when compared to the controls. Average seedling emergence was significantly lower in the herbicide-only plots when compared to the seeded-only plots as well (Fig. 2.5, Table 2.4). As hypothesized, *Bromus* emergence was lowest in the plots containing a combination of herbicide and native seed however; there was not a significant difference between these plots and the herbicide-only plots.

Average *Bromus* emergence increased in all treatments by the second year post-application. However, analysis of the difference in average emergence of seedlings between plots from the first and second years following treatment application (2007 and 2008), revealed no significant findings ($df = 47$, $f = 0.394$, $p = 0.781$). There was also no significant treatment effect when analyzing average emerged seedlings for just 2008 ($df = 47$, $f = 2.130$, $p = 0.105$) (Fig. 2.5).

Native Seed Performance at the Pinyon-Juniper Site

Emergence of seeded native species was negligible both in 2007 and 2008 (Table 2.5). In the first year, only 22 seedlings emerged from the soil samples among all the treatments representing less than 0.5% of total community composition. In the second year, there was nearly a five-fold increase (85 seedlings) in total seeded species emergence, but seeded species were still a minor component of the seed bank (1.9% of total community composition). The overall increase in emergence was largely driven by *S. cryptandrus* which represented 86% of total seeded native species emergence. To aid in analysis, all seeded species were grouped together. In 2007, there was an overall treatment effect ($df = 47$, $f = 4.011$, $p = 0.014$) with the seeded-only plots having

significantly more emergence of seeded native seedlings than the herbicide-only plots (Fig. 2.6). In 2008, an overall treatment effect was still evident ($df = 47$, $f = 2.944$, $p = 0.014$), but no significant pairwise comparisons were found.

Effects of Imazapic at the Shrub-Grassland Site

Bromus emergence was extremely low in both the treated and untreated plots during all years of collection (Table 2.4). Analysis of average emerged seedlings found no significant treatment effects for any given year (2006: $df = 59$, $f = 1.000$, $p = 1.000$; 2007: $df = 59$, $f = 0.861$, $p = 0.502$; 2008: $df = 59$, $f = 1.000$, $p = 1.000$).

Discussion

Effects of Imazapic at the Pinyon-Juniper Site

Low pre-treatment *Bromus* counts were expected at this site. In pinyon-juniper woodlands, several studies have documented the tendency of seeds to accumulate more in the litter layer beneath the canopy of trees and shrubs than in interstitial spaces (Evans and Young 1975; Nelson and Chew 1977; Koniak and Everett 1982; Paintner 1990). The rate of consumption of the litter layer by the fire was high, so presumably, the majority of seeds present on the site would likewise have been destroyed. Furthermore, many of the surviving seeds germinated before sampling occurred as a result of increased moisture during the monsoon rain season. We took soil samples after the monsoons in attempt to capture seeds from the whole community.

For studies focused solely upon *Bromus*, collections made past the after-ripening phase, but before the monsoons would capture the vast majority of seeds and provide a

picture of total possible germination. This knowledge would be useful in deciding whether or not additional measures, such as herbicide application, should be taken to advance recovery in disturbed areas. If a disturbance (i.e. thinning, prescribed fire) is planned for an area, this same knowledge would provide managers insight on what to expect regarding *Bromus* release following such an action. The close correlation between summer seed crops and *Bromus* emergence could allow seed bank assays to supplant aboveground assessments. Access to a greenhouse facility would be necessary, but field collections would require less time and personnel and soils can be stored for several years with little effect on seed viability.

Following treatment, sprayed plots at the pinyon-juniper site showed significant decreases in *Bromus* counts within one year of application. This is consistent with the findings of previous research (Bekedam 2005; Vollmer and Vollmer 2006; Kyser et al. 2007; Baker et al. 2009). Our hypothesis that imazapic would begin to lose effectiveness in the second year of the study was also affirmed. By 2008, nearly all sprayed plots showed some level of increase in *Bromus* emergence. In particular, plots receiving only herbicide averaged higher counts of emerged seedlings than the seeded-only plots and there was no longer a significant difference in the average number of emerged seedlings between any treatments. In the first year following treatment, herbicide-only plots averaged three quarters less *Bromus* than the controls. By the second year, these plots showed only about a 50% reduction of *Bromus*. This is an important result because to date, studies using imazapic to control *Bromus* have mostly focused on differing rates of

the herbicide and their immediate effects. Results of monitoring past the first year of application are rare in the literature.

In general, our findings are in agreement with others (Shinn and Thill 2002, 2004; Kyser et al. 2007; Baker et al. 2009) that imazapic is a reasonable option for creating a restoration window in highly invaded areas. However, the resurgence of *Bromus* in the second year following herbicide application indicates the need for subsequent treatments barring the successful establishment of native species within this time-frame.

Native Seed Performance at the Pinyon-Juniper Site

The success of the seeded native species was more difficult to elucidate. Our hypothesis that seed additions alone would not be sufficient in suppressing *Bromus* dominance was supported. Average *Bromus* emergence was lower in seeded-only plots than in the controls, but not significantly lower. Likewise, our belief that an herbicide-induced reduction of *Bromus* in the combined plots would yield higher rates of seeded native species establishment, thereby reducing the amount of space available for emergence from surviving *Bromus* seed, appeared to be substantiated given that these plots had the lowest average numbers in both years. What is puzzling though is the lack of correlation between *Bromus* emergence and emergence of seeded species in the greenhouse. In both years of the study, very few individuals emerged regardless of treatment and most of the emergence was from seeded-only plots. In the combined plots, where we expected to see higher numbers, only four individuals emerged in 2007

and only two emerged in 2008. The disparity in levels of *Bromus* control and seeded native species emergence may be due in part to the herbicide. The higher rate of emergence in the seeded-only plots suggests that a negative interaction with imazapic may have occurred in the combined plots.

Imazapic is effective at killing *Bromus*, but is by no means selective to annual grasses. Its mode of action is to inhibit an enzyme necessary for cell development and synthesis of proteins (Tu et al. 2001). Mature, perennial plants can often survive contact with the herbicide, but actively growing seedlings usually die. All seedlings emerging from the seed bank within the active period of imazapic would likely suffer adverse effects. Currently, research assessing the effects of imazapic on native species is limited. Trials conducted by Monaco et al. (2005) found perennial grasses responded favorably when imazapic was applied in the fall to control *Taeniatherum caput-medusae* (medusahead), but that response was better at lower rates. Sheley et al. (2007) also utilized imazapic to control *T. caput-medusae* and simultaneously monitored effects on seven seeded grass species. Results were varied with some species like *E. elymoides*, seeming to increase at higher rates while others did better in the absence of imazapic. In Zion National Park, *E. elymoides* decreased as imazapic rates were increased (De La Cruz 2008). A study in Colorado aimed at reducing cheatgrass in an *Artemisia tridentata* shrubland found imazapic to have detrimental effects on native forbs and two perennial grass species (Baker et al. 2009). Again though, some natives were unaffected. Results from a co-occurring aboveground study mirror our findings in that the density and

biomass of seeded native species is far higher in seeded-only plots as compared to combined treatment plots (Thode et al. 2010).

The fact that imazapic can deter native species suggests its culpability in curtailing emergence in this study, but the varied effects of imazapic leaves room for other possibilities. For example, different soil textures, soil moisture and soil biota assemblages all have the potential to affect how herbicide interacts with vegetation (Bekedam 2005). There is also a strong possibility that low soil moisture played a role in the overall poor performance of the seeded species. In 2008, precipitation was below average throughout the entire growing season (Fig. 3.2). Lack of adequate precipitation is a common culprit when seeding projects fail (Hessing and Johnson 1982; Koniak 1983; Brooks 2005). Greenhouse conditions and seed viability were likely not confounding factors as pre-study greenhouse trials using seed from the seed mix demonstrated a very high emergence rate for all species. However, in the field, it often takes about two years for seeded, perennial species to establish (Kephart and Amme 1992). It is therefore probable that our soil samples captured fewer seeds in 2007 because there were fewer seeds in the seed bank. However, the fact that numbers of emerging seedlings were still low in 2008 suggests that these species had yet to become successfully established and therefore, were contributing only minimal amounts of seed to the soil seed bank.

Additional scrutiny of the literature pertaining to the seeded native species revealed that *E. elymoides* and other members of the tribe *Hordeae* are known to be

fairly resistant to imazapic (Shinn and Thill 2004; Kyser et al. 2007; Baker et al. 2009). Also, germination of *P. palmeri* seeds may have been restricted as a result of the soil preparation process as inhibition of this species does occasionally occur when undergoing cold-stratification (Kitchen and Meyer 1991). As previously mentioned, seeds from the seed mix performed admirably during initial greenhouse trials, but these seeds were taken directly from seed sacks and were not stratified. Suspicion of a negative interaction with imazapic is better founded when examining *S. cryptandrus* and *S. ambigua*. Dela Cruz et al. (2008) found that in greenhouse trials in Zion National Park, *S. cryptandrus* germination was reduced at various rates of imazapic especially in the absence of mulch. In this study, the observed increase in this species in 2008 occurred almost exclusively in the unsprayed, seeded-only plots. Regarding *S. ambigua*, studies have found members of the genus *Sphaeralcea* to perform poorly when exposed to imazapic (Baker et al. 2009; Owen et al. 2009). However, it is still unclear if the herbicide was affecting seeded native species emergence.

Despite possible negative interactions with imazapic, the results of this study reflect what other studies have reported which is that competition from nonnative, annual bromes often needs to be mitigated in order for post-fire seeding with native species to be effective (Humphrey and Schupp 2002; Brooks 2005; Davison and Smith 2007). For example, *Bromus* emergence was lower in seeded-only plots than the controls, but the difference was not significant. Seeding with natives has had success in areas invaded by other exotics, such as *Carduus nutans* (musk thistle) (Goodrich and Rooks 1999; Floyd et al. 2006). However, the best examples of post-fire recovery have

occurred in healthy pre-disturbance stands where propagule survival was adequate enough to foster quick revegetation through seed germination and resprouting of perennial species (Hessing and Johnson 1982; Everett and Ward 1984; Jones 1998; Harper et al. 2003; Allen et al. 2008)

Discounting issues with herbicide and invasive species, the principle problem of native seeding operations revolves around the fate of seed upon dispersal. Variable precipitation, granivory, soil conditions and a host of other factors can greatly widen the gap between the amount applied and what is actually available for germination (Thatcher and Hart 1974; Linhart 1976; Robocker and Schirman 1976; Hessing and Johnson 1982; Koniak 1983; Brooks 2005). The problems associated with assisted native establishment may seem to be insurmountable, but there is still a trend to counter post-fire vegetation losses with native seeding operations due both to new research discoveries (Belnap et al. 2003; Meyer et al. 2007; Leger 2008) and the basic need to repopulate depauperate seed banks following large-scale disturbance (Koniak and Everett 1982; Allen et al. 2008; Allen and Nowak 2008). This study found that *S. cryptandrus* outperformed the other species in the seed mix. The abundant production of small, hard-coated seed make it ideal for surviving harsh conditions and quick establishment when conditions are more favorable for growth. Also, it is compelling that studies in Colorado (Costello 1944; Coffin and Lauenroth 1989), New Mexico (Henderson et al. 1988), Kansas and Nebraska (Weaver and Mueller 1942; Abrams 1988) and western Utah (Humphrey and Schupp 2001) have all reported *S. cryptandrus* to be one of the few perennial grasses consistently found in the persistent seed bank. The

prevalence of this species in the Western United States combined with its ability to stock the seed bank advocates for its inclusion into more seed mixes. Finding additional species that have similar traits would also be useful.

Effects of Imazapic at the Shrub-grassland site

The low numbers of *Bromus* seedlings emerging from soil samples taken from this site make it difficult to draw any conclusions from the data. It is not known if brome species were present in any great numbers at this site prior to the fire. Following the fire, large populations of *B. tectorum* were found in close proximity to the study area, but few plants were observed within the plots themselves. However, based upon previous studies, it was assumed that the site had a high potential for a post-fire invasion from nearby seed sources (Young et al. 1976; Jessop and Anderson 2007). The proliferation of two perennial species that did not show up in the seed bank study, *Convolvulus arvensis* (field bindweed) and *Pleuraphis jamesii* (galleta grass) may have helped prevent this from happening. *C. arvensis* is an aggressive exotic that easily resprouts from an extensive root system (DeGennaro and Weller 1984). *P. jamesii* is a native grass that resprouts from rhizomes following fire and can surpass pre-fire populations within two years given adequate moisture (Jameson 1962; Humphrey and Schupp 1999). Plant invasions are contingent upon minimal competition for available resources (Davis et al. 2000). The fast recovery of *C. arvensis* and *P. jamesii*, presumably monopolized space, water and nutrients before *B. tectorum* could successfully occupy the site. Other studies have discussed the immediate return of pre-burn, mid-seral

species and consequent lack of early seral species establishment (Young et al. 1976; Connell and Slatyer 1977; Everett and Ward 1984).

Another contributing factor could be the high clay content of the soil. *B. tectorum* has the ability to grow in many different soil types, but establishes better in coarser textured soils than in finer clays and clay loams (Doescher et al 1986). In conjunction with the clay soils, there is evidence of soil erosion, including sheeting and rilling, across the entire study site. An overall scarcity of seed reserves of any species suggests that monsoonal precipitation may be acting as a secondary dispersal agent by washing seeds into the numerous gullies present on the site where they are subsequently transported out of the system. A small body of literature has documented the role of water in long-distance seed transport (Reichman 1984; Matlack 1989; Chambers and MacMahon 1994; Griffith and Forseth 2002; Vander Wall et al. 2005).

Conclusion

This study demonstrates that imazapic can be quite effective at providing short-term control of *Bromus* in the soil seed bank. However, given the expense of application, lack of long-term control and possible negative impacts on the seeded native species, prudence is recommended when deciding if imazapic is the correct choice for achieving management goals. There still remains a need for finding better ways to restore *Bromus* dominated systems. Use of the herbicide imazapic shows promise, but further research needs to be conducted both on the susceptibility of native species in general and on the timing of seeding additions in relation to imazapic applications. Finding site-adapted natives that can quickly replenish fire-impooverished

seed banks would also be beneficial. This study and others indicate that *S. cryptandrus* may be able to fulfill this role in areas where it naturally grows. This study also suggests potential for seed bank assays in guiding management decisions and monitoring restoration actions. Examination of the soil seed bank following treatments strengthened the results produced by the complementary aboveground study. We demonstrated that at the study area, imazapic had an adverse affect on *Bromus* in the seed bank, and greatly reduced the threat of recruitment from this source in the following season. Seed bank assays of *Bromus* also allow for a reasonable prediction of next year's *Bromus* crop.

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Table 2.1. Descriptions of location, treatment, vegetation, soil, elevation and associated plant species for the two study sites.

Site	Treatments	# of replicates	# of plots	Soil	Elevation (m)
Pinyon-Juniper	Herbicide and Seeding	12	48	Very Cobbly Loam	1340-1500
Shrub-Grassland	Herbicide	30	60	Clovis Fine Sandy Loam	1350-1380

Table 2.2. Native species used in the seed mix.

Seeded Species	Common Name	Life Form
<i>Elymus elymoides</i>	bottlebrush squirreltail	Grass
<i>Penstemon palmeri</i>	Palmer penstemon	Forb
<i>Sphaeralcea ambigua</i>	desert mallow	Forb
<i>Sporobolus cryptandrus</i>	sand dropseed	grass

Table 2.3 List of samples compromised during treatment application. A sample represents a composite of two subsamples. There are ten samples per plot.

Block #	Intended Treatment	# of samples compromised	Reason Compromised
1	control	3	received herbicide
4	herbicide-only	3	did not receive herbicide
4	combined	3	did not receive herbicide
7	herbicide-only	6	did not receive herbicide
10	control	2	received herbicide
11	herbicide-only	4	did not receive herbicide
12	herbicide-only	1	did not receive herbicide
12	combined	2	did not receive herbicide
Total		24	

Table 2.4. Total emerged *Bromus* seedlings for each treatment by site and year. No seeding treatments were applied at the shrub-grassland site. Numbers in parentheses represent estimated seeds/m². Letters show significant treatment effects within each year.

Site	Year	Treatment			
		Control	Seeded	Herbicide	Combined
Pinyon-Juniper	2006	6 (107.16) ^a	11 (196.46) ^a	4 (71.44) ^a	4 (71.44) ^a
	2007	540 (9,900.92) ^a	298 (5,322.28) ^a	122 (2,205.33) ^b	42 (853.86) ^b
	2008	735 (14,028.08) ^a	446 (7,965.56) ^a	476 (8,610.36) ^a	186 (3,447.93) ^a
Shrub-Grassland	2006	-	-	1 (176.68)	-
	2007	5 (883.40)	-	13 (2,296.84)	-
	2008	-	-	1 (176.68)	-

Table 2.5. Total emerged seeded species seedlings for each treatment by site and year (pinyon-juniper site)

Species	Control	Seeded	Herbicide	Combined
2007				
<i>Elymus elymoides</i>	1	7	0	1
<i>Penstemon palmeri</i>	1	6	0	3
<i>Sphaeralcea ambigua</i>	0	0	0	0
<i>Sporobolus cryptandrus</i>	1	1	1	0
Total	3	14	1	4
Seeds/m²	53.58	250.04	17.86	71.44
2008				
<i>Elymus elymoides</i>	2	0	2	0
<i>Penstemon palmeri</i>	2	0	0	0
<i>Sphaeralcea ambigua</i>	2	3	1	0
<i>Sporobolus cryptandrus</i>	5	64	2	2
Total	11	67	5	2
Seeds/m²	203.87	1,196.92	149.53	35.72

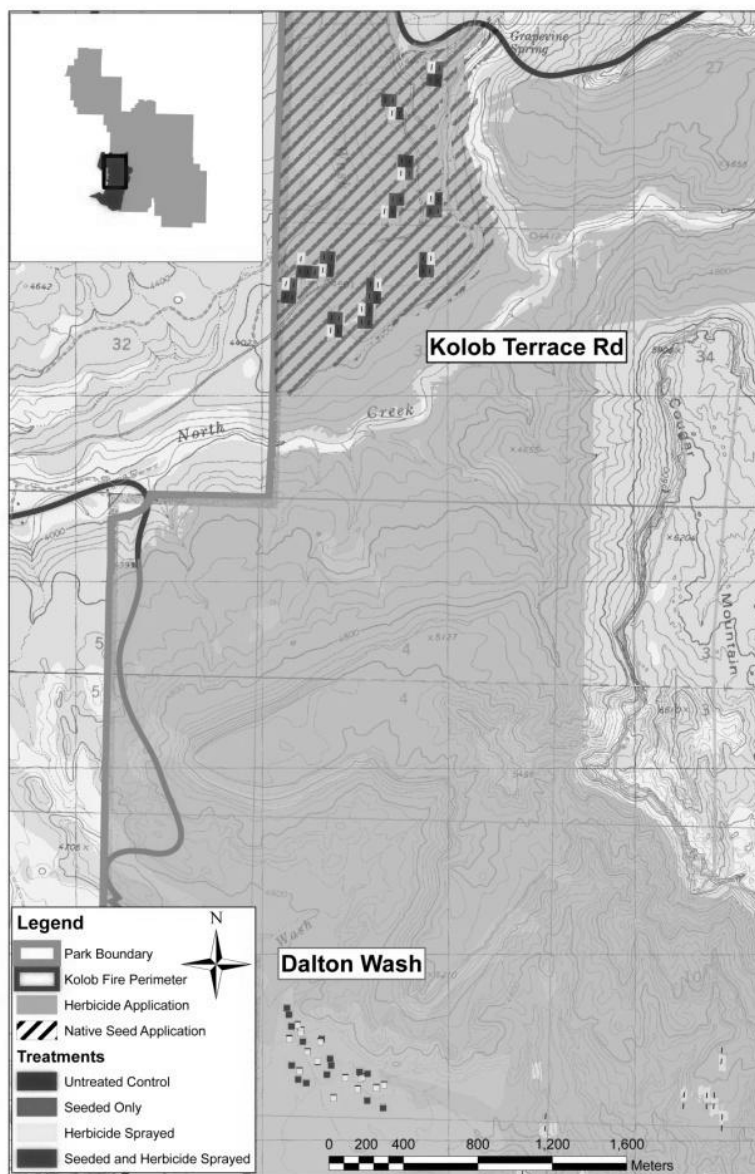


Figure 2.1. Overview of the two study sites. The shaded area represents the herbicide treatment. Diagonal lines show the extent of the seeding treatment.

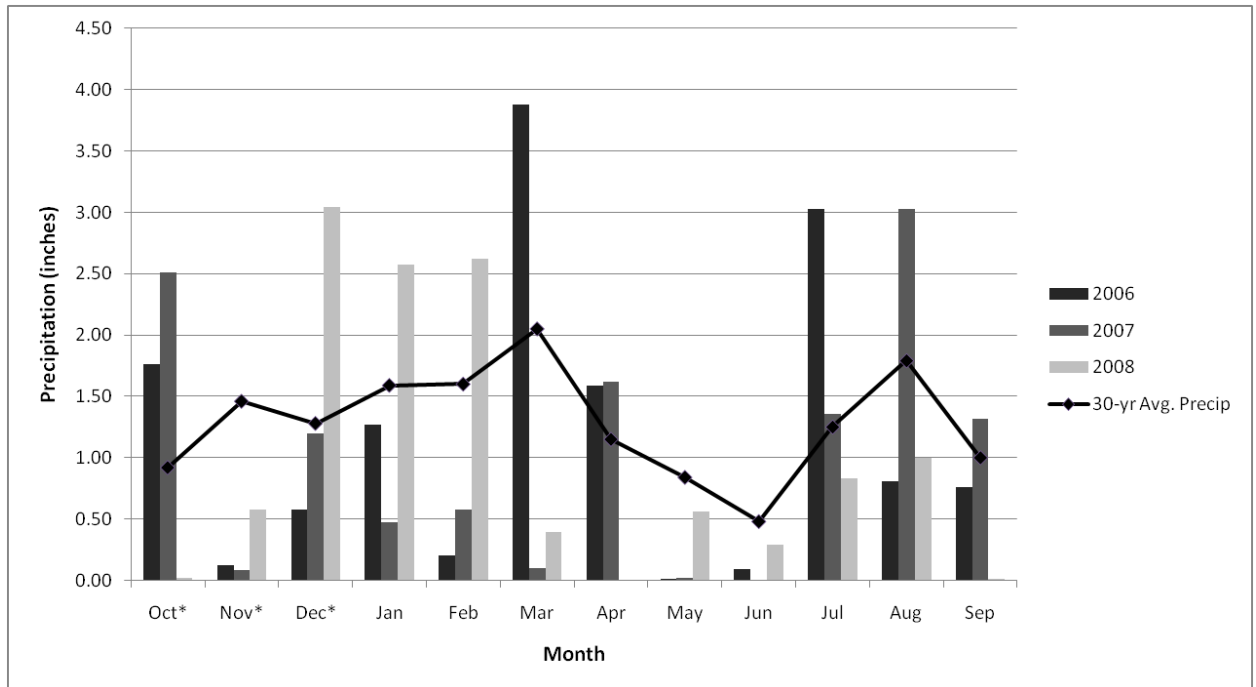


Figure 2.2. Monthly precipitation for water-years 2006, 2007 and 2008 and 30 year average at Zion National Park, Washington Co., Utah.

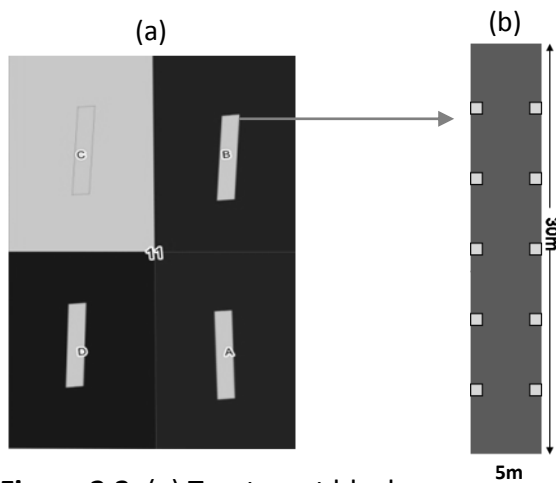


Figure 2.3. (a) Treatment block showing 5x30m plots surrounded by 15-m buffers. Each block contains 4 plots with a random treatment assignment (control, seeded, herbicide, seeded & herbicide). (b) Close-up of plot with 1-m squares showing soil sampling locations.

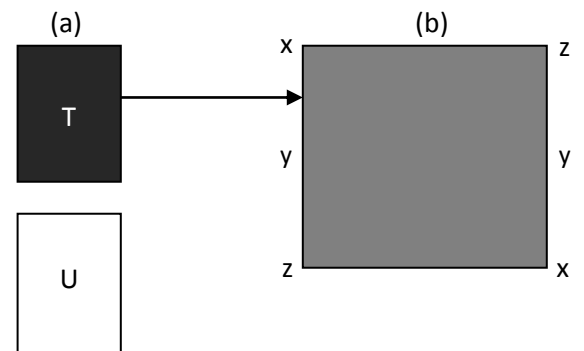


Figure 2.4. (a) Pair of 2x2-m plots. At random, one plot in each pair was treated with herbicide (T) while the other was left as an untreated control (U). (b) Plot Detail showing soil sampling locations: X (2006), Y (2007), Z (2008).

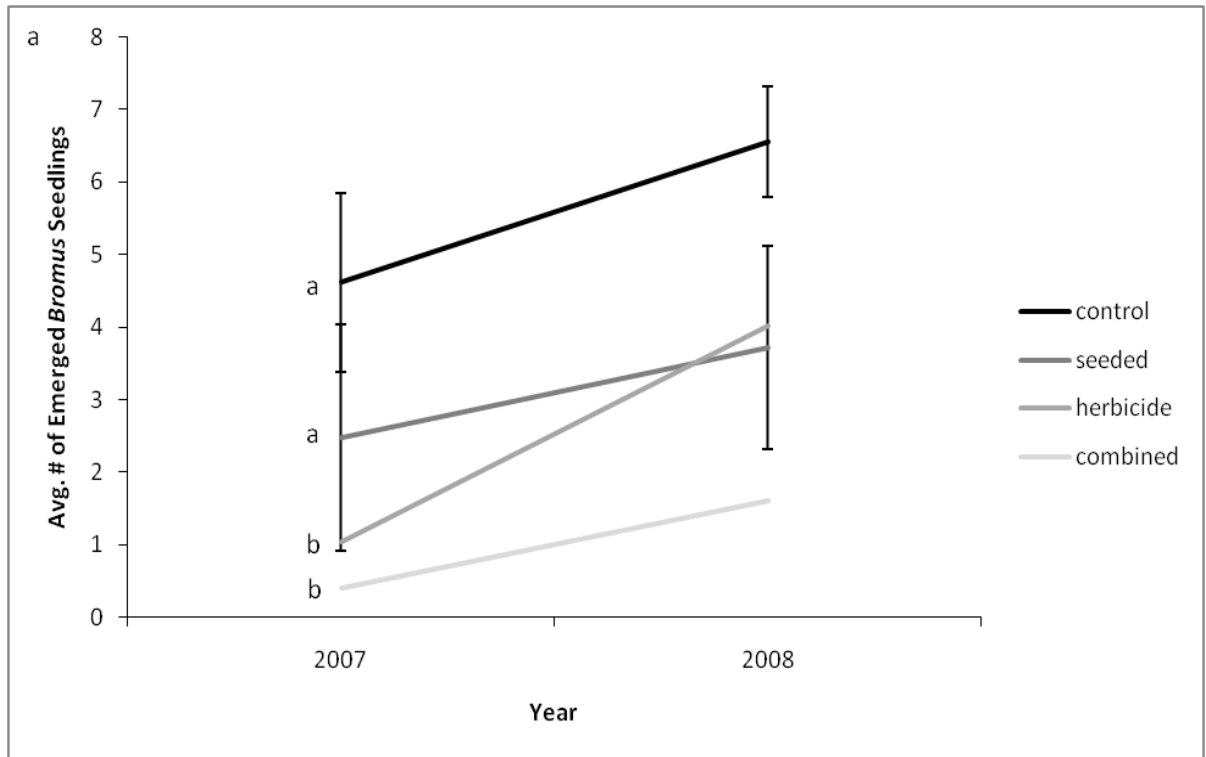


Figure 2.5. Comparison of average emerged Bromus seedlings, by treatment, for 2007 and 2008 with standard error bars. Means sharing a letter do not differ at $p < 0.05$. Letters indicate significant treatment effects within each year.

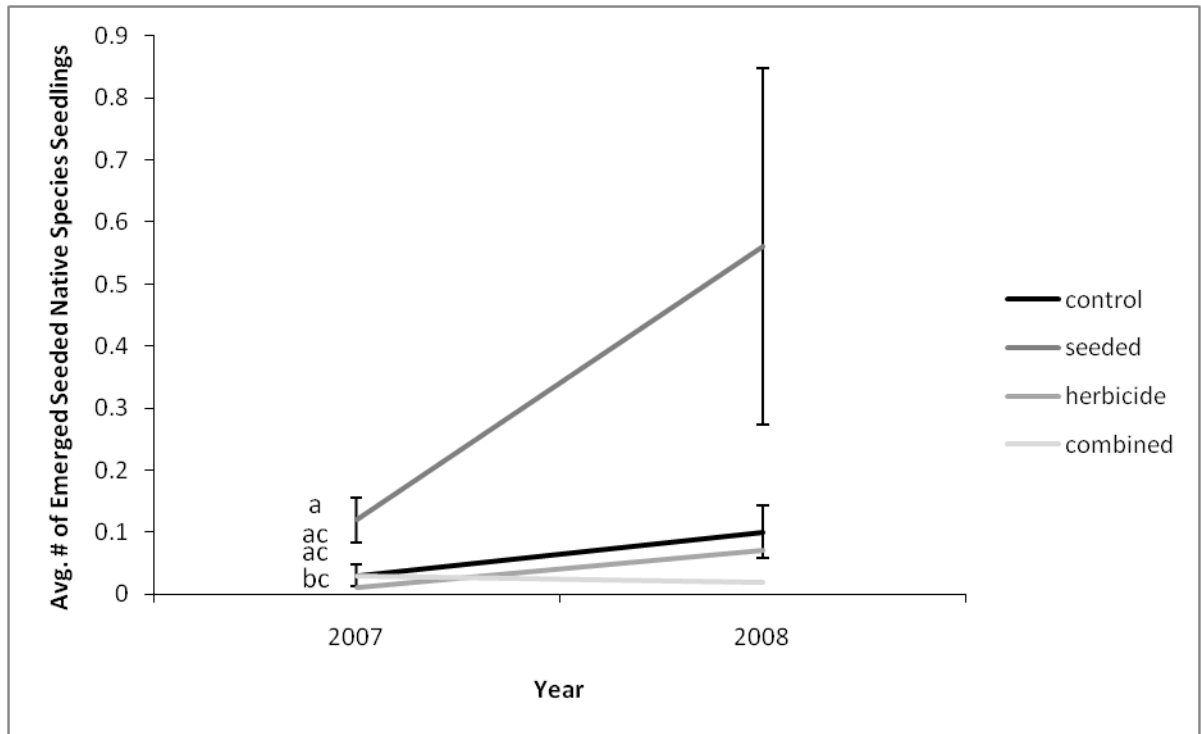


Figure 2.6. Comparison of average emerged seeded native species seedlings, by treatment, for 2007 and 2008 with standard error bars. Means sharing a letter do not differ at $p < 0.05$. Letters indicate significant treatment effects within each year.

Chapter 3

Soil Seed Bank Composition Following Fire, Native Seeding and Herbicide in Pinyon-Juniper Woodland

Abstract

In recent years, the herbicide imazapic has been used to successfully control annual, nonnative plant species in non-agricultural, wildland settings. The alleviation of competition within invaded sites can allow for the reestablishment of more desirable native species. In nearly every study involving imazapic however, there has been at least some incidental control of non-target species. The effects of imazapic are often site-specific and vary depending upon dosage, environmental conditions and the composition of onsite vegetation communities. In addition, studies monitoring ancillary effects are not common and even rarer are studies examining effects as they apply to the soil seed bank. In an attempt to add to contemporary knowledge, this study analyzed the impacts of imazapic and a native seed mix on a soil seed bank community in Zion National Park following a large wildfire. The restoration treatments were designed to prevent a large-scale invasion of the burned area by invasive, nonnative, annual *Bromus* species. The effects of imazapic on the community were not pronounced, but several annual, forb species were significantly reduced in plots treated with herbicide. Emergence of seeded species was low throughout the study and had little observable impact on the greater soil seed bank community. Overall, emergence

and frequency of species showed little difference in the control plots as compared to treated plots following the removal of the target brome species from the analysis.

Introduction

Soil seed banks represent the spacial accumulation of seeds within the soil profile and on the soil surface (Paintner 1990). In semiarid environments, the majority of seeds occupy the litter layer and the top 2-3 cm of the soil (Nelson and Chew 1977; Koniak and Everett 1982). Seed banks vary spatially and temporally with inputs arriving and departing throughout the year and seed accumulation occurring at different points of the soil profile and at different locations on the landscape (Coffin and Lauenroth 1989; Simpson et al. 1989). High seed densities are correlated with recent disturbance and numbers tend to decline as succession proceeds (Olmsted and Curtis 1947). Similarly, correspondence between aboveground and belowground composition diminishes through the passage of time (Chippindale and Milton 1934; Paintner 1990; Abella et al. 2007). In pinyon-juniper woodlands, seeds generally accumulate more in the litter layer beneath canopy and shrub species than in interstitial spaces. This is due in part to conditions that favor herbaceous growth, thus amplifying seed rain at these microsites (Nelson and Chew 1977; Young and Evans 1978). The litter layer is also effective at trapping seeds being transported by surface runoff and wind (Chambers and MacMahon 1994; Griffith and Forseth 2002). Species composition in the seed bank fluctuates depending upon location but is usually comprised of numerous annual and biennial species and few perennials. Annual species can make up to 80-90% of the seed

bank community (Allen et al. 2008). Unlike understory vegetation, seed bank composition and density is not affected by tree density (Allen and Nowak 2008).

Until recently, fire was not a common occurrence in pinyon-juniper (Floyd et al. 2006). Species adapted to fire do occur in these woodlands, but the seed bank is largely populated by annual obligate seeder species (Allen et al. 2008). Fire-free intervals may last as long as 400 years, but when fires do ignite, they are often high-intensity, stand-replacing events (Miller and Tausch 2001). The preponderance of seed in the litter and organic layers compromises seed survivorship. Even so, fire can affect seed banks in multiple ways and does not necessarily cause a complete depletion of seed reserves. Most seeds on the soil surface will be consumed by fire, but those resting even just below the surface may survive due the insulating properties of mineral soil or the seed coat itself (Keddy et al. 1989). Other seeds respond to fire and germinate following some interaction of cues including heat shock, smoke, charred wood, light and temperature (Auld and Denham 2006). Seeds that do persist can greatly shape the structure of the immediate post-fire community. On one end of the spectrum, pre-fire assemblages may be reinstated within one year following a fire. Dwyer and Pieper (1967) monitored understory vegetation following a fire in south central New Mexico. The fire appeared to have no affect on forb or grass composition. In this case, regeneration was primarily vegetative and the seed bank had little effect on succession. Conversely, a study in Utah delivered disturbing results regarding succession and the invasive grass, *Bromus tectorum* (cheatgrass). Surveys of the aboveground community found little evidence of *B. tectorum* emergence. The seed bank however, contained

large amounts of seed even under unburned, late-seral vegetation. A fire removed much of the seed, but what remained was sufficient to double the population one year after the fire. Inputs from other species were limited (Hassan and West 1986). This is a common trend in the West and even when fire regimes remain consistent with historical patterns, the seed bank and resulting herbaceous understory assemblage may be shifting more towards exotics in many pinyon-juniper woodlands (Floyd et al. 2006; Humphrey and Schupp 1999; Young and Evans 1978).

The current preponderance of invasive species in the West has necessitated the need for integrated approaches to post-fire restoration (Brown et al. 2008; Humphrey and Schupp 2002). Efforts to replenish seed banks with seeding alone often fail due in large part to competition from nonnative species (Brooks 2005; Davison and Smith 2007). Previous methods for mitigating the threat of exotics prior to seeding have had mixed results, but are often not sufficient, especially when trying to control aggressive species like *B. tectorum* (Canode et al 1962; Evans et al. 1970; Stewart and Hull 1949). As pinyon-Juniper woodlands are highly prone to invasion from *B. tectorum*, its control is of paramount importance to restoration efforts. In recent years, the herbicide imazapic (Plateau®) has proven to provide acceptable, short-term control (Baker et al 2009; Bekedam 2005; Kyser et al 2007; Matchett et al 2009; Vollmer and Vollmer 2006). More research is warranted however as this herbicide often impacts native vegetation as well (Dela Cruz 2008; Monaco 2005, Sheley et al. 2007). Few studies have monitored the effects of imazapic on native plants. Pekas (2010) is to our knowledge the only study to analyze the repercussions of imazapic on the soil seed bank. This study concluded

that species composition within the germinable seed bank shifted in response to imazapic regardless of fire effects, but overall, the changes were not significant and dominant pre-treatment species were mostly unaffected. In our study, we examined the seed bank of a pinyon-juniper woodland following a wildfire in Zion National Park. To assist native reestablishment and prevent invasion from exotic annual bromes, the study site was treated with imazapic as well as a native seed mix.

Our main objective was to determine non-target seed bank response to the treatments during each year of the study. We hypothesized that 1) imazapic would reduce the density of annual species in the sprayed plots as compared to the controls or plots treated only with the native seed mix and 2) in the second year following treatments, plots treated with both herbicide and seed would have greater native, perennial species density than the controls or plots with a single treatment. A second objective was to present descriptive data from this study in order to add to the limited knowledge of the role of seed banks in shaping the aboveground community following fire in pinyon-juniper woodlands.

Methods

Site Description

This study was conducted within the Kolob burn, which started in June 2006 near the southwest corner of Zion National Park in southern Utah (37°9.38' N, 113°29.35'W). The fire burned 4,256 hectares, the majority (75%) being in pinyon-juniper woodland, the remainder in shrub/grassland and ponderosa pine. Based on the thirty-year average, the average annual temperature for this region is 16° C with 37 days over 38° C and 74

days below 0° C. There are 62 days of measurable precipitation per year, 4 of which are snow. Annual precipitation averages 38 cm, the majority of which falls during the winter (October-April) and averages 25 cm (Western Regional Climate Center 2005). During the study period, annual precipitation was slightly below average in all years of the study. The first two years (2006 & 2007) exhibited similar patterns with most moisture arriving in October of the previous year and late spring/early summer (although, more precipitation fell in the monsoonal months of July and August during 2007). Winter moisture (December, January, and February) was the major contributor in 2008 with far less precipitation falling during the late summer monsoons than occurred in 2006 or 2007.

One study site was selected and was located in pinyon-juniper woodland. The site is dominated by *Pinus monophylla* (singleleaf pinyon) and *Juniperus osteosperma* (Utah juniper). Understory species include *Artemesia tridentata* (big sagebrush), *Amelanchier utahensis* (Utah serviceberry) and *Purshia mexicana* (cliffrose). Soils are well drained and consist of very cobbly loam within the top 5 cm and gravelly clay loam from 5-12.5 cm. Parent material consists of eolian deposits derived from shale and sandstone over residuum weathered from basalt. Slopes range from 2-20 percent.

Imazapic was applied via helicopter to 3,577 ha at a recommended rate of 0.59L/ha. Previous pre-fire vegetation mapping found both *B. tectorum* and another invasive annual, *Bromus rubens* (red brome) in 70% of plots visited within the burned area. (Kolob Fire Emergency Stabilization and Burned Area Rehabilitation Plan, 2006). Seed reserves of native species were likely scarce given the long-term presence of these

exotics and their ability to monopolize the soil seed bank. To assist native succession, this region received an additional aerial application (9.1 kg/ha) of a native seed mix comprised of *Sporobolus cryptandrus* (sand dropseed), *Elymus elymoides* (bottlebrush squirreltail), *Penstemon palmeri* (Palmer penstemon) and *Sphaeralcea ambigua* (desert mallow). All species are perennial, had a pre-fire presence and have some ability to compete with *B. tectorum* (Humphrey and Schupp 2004; Leger 2008).

Study Site Design

Initial site selection was based upon stratification of the burned area by treatment type, high burn severity, vegetation type and geological groupings with the goal of reducing onsite environmental variability. This site contained a total of 48 plots. A randomized block design was implemented with each block containing four plots for a total of 12 blocks. Plots are 5 x 30 m and contain one of the following randomly assigned treatments: control, seeded-only, herbicide-only or a combination of seed and herbicide. A 15-m buffer was established around each plot to aid in accurate aerial treatment application. Individual plots are separated by at least 30 m and no buffers are closer than 15 m to any road. Seeded plots were hand-seeded at a rate consistent with the aerial application to insure precision.

Seed Bank Sampling

Seed bank collection was done in late October-early November when soil seed reserves were most replete with available annual and perennial species. Samples were obtained at 5-m intervals (5, 10, 15, 20, and 25 m) along the west and east side of each vegetation plot for a total of 480 samples. A sample consisted of a composite of two

smaller sub-samples taken from around the perimeter of a 1-m quadrat. Due to inconsistencies in the aerial application of the herbicide treatment, 24 of the 480 samples were not utilized as a result of misapplication. To help overcome the spatial anomalies inherent in belowground seed distribution, collection of numerous, small samples was preferred to taking only a few large samples (Bossuyt et al 2007). However, the tendency of seeds to be clumped around a parent plant can still lead to an underestimation of species composition when samples fall within seed scarce regions between plants (Bigwood and Inouye 1988).

Initial samples were collected by pressing a tin soil canister (height 4.4 cm, diameter 6.0 cm) into the ground to a depth of 3.0 cm (85 ml sample). A metal spatula was then inserted underneath the canister to aid in the removal of a complete sample. Sampling was restricted to the top 3 cm of the soil as previous studies have found few seeds present below 2-3 cm in desert soils (Price and Reichman 1987; Ferrandis et al 2001; Kemp 1989). Obstructions such as rocks and woody debris (exceeding 1 inch in diameter) were picked up (with any external soil being brushed into the canister) and placed to the side. Standing vegetation was also avoided. Samples were then placed into a labeled bag and transported back to Flagstaff, AZ where they were placed outside in sealed, plastic containers for 2-3 months in order to vernalize the seeds. Outside conditions ranged from below freezing to 5° C. Samples were later brought into the greenhouse to be processed for the seed bank emergence portion of the study. The greenhouse was not kept a constant temperature. Temperatures ranged from a low of

5° C to a high of 20° C during the winter months and 10° C to 30° C in the summer. No artificial lights were used.

Seed Bank Determination

The contents of the seed bank were ascertained using the emergence method standardized by the US Geological Survey, Western Ecological Research Center. These protocols are based on earlier methods used in the Great Basin (Young et al. 1969, Evans and Young 1975, and Young et al. 1981), but were modified to capture annual plants found in the Mojave Desert (T. Esque et al. unpublished data). Many of these same annuals proliferate at our sites as well. Soils were brought out of storage, air-dried and ran through a 2 mm mesh sieve. Stones and organic debris were discarded after first removing any adhering soil. A ½ cup of the sifted sample was then mixed with ½ cup of Vermiculite to increase water retention. Each mix was placed in a 6 inch bulb pot lined with synthetic weedblock fabric. Pots were randomly placed on greenhouse benches and watered. Seedlings were identified, tallied and plucked as they emerged. This process continued until germination had mostly ceased (4-6 weeks). The soil mixtures were allowed to dry out for 2-3 weeks followed by a second watering phase (3-4 weeks).

This pattern was repeated two more times with potassium nitrate (50 ml per pot/0.01 M solution) being added at the beginning of the third phase (2-3 weeks) and Gibberellic acid (50 ml per pot/ 6.5×10^{-4} M solution) added at the beginning of the fourth phase (2-3 weeks). The dry-down period approximates natural moisture fluctuations necessary for germination to occur in some desert species (Baskin and Baskin 1998;

Meyer et al. 2007). The chemical additives are not actual treatments, but have been included due to their previously documented ability to stimulate germination in perennial species (Baskin and Baskin 1998; Bell et al 1995; Jones and Nielson 1992). Nomenclature for all emerging species followed USDA, NRCS (2009).

The number of seeds/m², were approximated by first determining the surface area of a soil canister (28.3 cm²). This number was multiplied by the total number of subsamples in a plot to determine the total surface area sampled. The area of one square meter was then divided by the total surface area sampled. The number of seeds emerging from each sample was multiplied by this result in order to estimate the number of seeds/m² (the multiplier varied by plot depending upon the amount of samples compromised during treatment application) (Warr et al. 1994). Finally, trial pots were set up in the greenhouse to test the viability of the seeded native species. Twenty seeds of each species were randomly selected from a seed sack and placed into individual bulb pots containing potting soil. Seedlings emerged from the majority of all seeds for all species.

Data Analysis

All analysis was performed using PC-ORD software (5.31). Permutational multivariate analysis of variance (PerMANOVA) was used to detect differences in composition across the four treatments. (Euclidean distance, 4,999 permutations). This analysis of variance technique generates an F-statistic using permutations of the observations, thus allowing for the inclusion of non-normal data and multiple distance measures (Anderson 2001). Detection of a significant treatment effect ($\alpha = 0.05$), was

followed by post-hoc pair-wise comparisons which allowed for a more detailed treatment analysis. PC-ORD does not correct the p values for multiple comparisons. Without a correction, the chance of committing a Type I error was increased to about 20%. However, use of the prescribed Bonferroni correction dramatically increased the probability of committing a Type II error. Based on the advice of a statistician (D. Laughlin, personal communication, April 2010) and current literature, we opted not to use the correction (Anderson 2001; Nakagawa 2004). In order to further elucidate the findings of the PerMANOVA tests, Indicator Species Analysis (ISA) was performed in order to detect which species were driving between-treatment differences. (Monte Carlo: 4,999 permutations). This test combines abundance and frequency values to produce an indicator value. Indicator values demonstrate the constancy and exclusiveness of a species to a given group. A Monte Carlo test determines the statistical significance of these values (McCune and Grace 2002). Finally, nonmetric multidimensional scaling (NMS) ordinations were used to visually assess patterns emerging from PerMANOVA and ISA.

Results

Treatment Effects on the Soil Seed Bank Community

A PerMANOVA analysis of the seed bank prior to treatment application (2006) revealed no significant within plot or between plot differences in the density of seedlings emerging from the soil samples. Similarly, an NMS ordination showed no observable trends in species abundance nor did plots appear to be sorting out along any

environmental gradient. Based upon this evidence and the fact that treatments had yet to be applied, we did not perform ISA on these data.

One year following treatment application (2007), there was no significant difference in the soil seed bank communities associated with each treatment type. However, an ISA of the entire community found three indicator species, all of which were indicators for the control group. All three species are native forbs and included; *Cryptantha gracilis* (narrowstem cryptantha), *Draba cuneifolia* (wedgeleaf draba) and *Silene antirrhina* (sleepy silene) (Table 3.1). The NMDS ordination required two dimensions in order to reach an acceptable stress level of 17.80. There was only a conservative amount of spatial separation within the data between the four treatments, but this separation is more apparent when comparing unsprayed plots (controls and seeded-only) to sprayed plots (herbicide-only and combined). Unsprayed plots are also clustered closer together than sprayed plots indicating more uniform composition. Finally, the majority of species appear to be more associated with the unsprayed plots (Fig. 3.1).

In the second year following treatment application (2008) there still was no significant difference in the communities associated with each treatment type. An ISA of the entire community revealed *D. cuneifolia* to be an indicator for the controls and *Sporobolus cryptandrus* (sand dropseed) to be an indicator for the seeded only plots (Table 3.1). The NMDS ordination could only find a one dimension solution and had a stress level of 40.8. This solution was not used as final stress values above 20 yield

graphs that are difficult to interpret and potentially misleading (McCune and Grace 2002).

To complement the overall community analyses and help characterize the seed bank community associated with each treatment we compiled data and ran additional PerMANOVA tests pertaining to life history, growth form, nativity and abundance.

Life History

The density of annual species emerging from the soil samples did not significantly differ between treatment types in either 2007 or 2008. The number of emerged seedlings in 2007 was highest in the control plots (1,361), followed by the seeded-only plots (919), the combined plots (604) and the herbicide-only plots (513) (Table 3.2). The four most abundant species for both the control and seeded-only plots were; *D. cuneifolia*, *Vulpia octoflora* (six weeks fescue), *S. antirrhina* and *Erodium cicutarium* (redstem stork's bill). In the herbicide-only plots they were; *D. cuneifolia*, *V. octoflora*, *Lotus humistratus* (foothill deervetch) and *Plantago patagonica* (wooly plantain) and in the combined-only plots they were; *D. cuneifolia*, *L. humistratus*, *V. octoflora* and *S. antirrhina*. In 2008, the number of emerged annual seedlings was highest in the herbicide-only plots (727), followed by the control plots (577), the seeded-only plots (549) and the combined plots (282). In the control and seeded-only plots, the four most abundant species were; *V. octoflora*, *D. cuneifolia*, *E. cicutarium* and *S. antirrhina*. In the herbicide-only plots they were; *V. octoflora*, *Lotus denticulatus* (riverbar bird's foot trefoil), *L. humistratus* and *D. Cuneifolia* and in the combined-only plots they were; *L. denticulatus*, *L. humistratus*, *V. octoflora* and *D. cuneifolia*.

The density of perennial species emerging from the soil samples was not significantly different in 2007, but we did find a significant treatment effect for 2008 ($F = 2.75$, $p = 0.021$) (Fig. 3.2). However, no pairwise comparisons were significant at $p < 0.05$. In 2007, emergence of any seeded species was very low. This pattern was repeated in 2008 for all species with exception of *S. cryptandrus* which had a five-fold increase in emerged seedlings.

Nativity

We did not find the density of nonnative species to be significantly different between treatment types in either 2007 or 2008. The number of emerged seedlings in 2007 was highest in the control plots (111), followed by the seeded-only plots (85), the combined plots (48) and the herbicide-only plots (43). The most abundant species for any treatment type was *E. cicutarium*. In 2008, the highest number of seedlings emerged from the control plots (184), followed by the herbicide-only plots (175), the seeded-only plots (152) and the combined plots (140). The most abundant species were *E. cicutarium* and *Lactuca serriola* (Table 3.2).

Growth Form

Looking at growth form, there was a significant treatment effect for forbs in 2007 ($F = 3.02$, $p = 0.04$), but not in 2008. This effect was most evident when comparing control plots to herbicide-only plots (Fig. 3.3). Emergence of grasses was not significantly different under any treatment type for either year. The number of forb seedlings emerging from the soil samples in 2007 were highest in the control plots (1037), followed by the seeded-only plots (622), the combined plots (513) and the

herbicide-only plots (341). The four most abundant species for the control, seeded-only and combined plots were: *D. cuneifolia*, *S. antirrhina*, *E. cicutarium* and *L. humistratus*. This was true for the herbicide-only plots as well except that *S. antirrhina* was replaced by *P. patagonica*. Forb seedlings emerged in 2008 were most numerous in the control plots (496), followed by the herbicide-only plots (451), the seeded-only plots (391) and the combined plots (330). The four most abundant species for the controls and seeded-only plots were *D. cuneifolia*, *E. cicutarium*, *S. antirrhina* and *L. humistratus*. For the herbicide-only and combined plots, they were *L. denticulatus*, *L. humistratus*, *D. cuneifolia* and *E. cicutarium*. The most abundant grass species for any treatment during either year was *V. octoflora*.

Treatment Effects on Individual Species

According to the ISA results for the entire community, several species were indicators for either the controls or the seeded-only treatment. We used PerMANOVA to further analyze these species. In 2007, *S. antirrhina*, *C. gracilis* and *D. cuneifolia* were all indicators for the controls. Of these, a significant treatment effect was evident only for *D. cuneifolia* ($F = 3.14$, $p = 0.018$). Emergence of *D. cuneifolia* seedlings was significantly higher in the control plots and seeded-only plots as compared to the herbicide-only plots (Fig. 3.4). By 2008, only *D. cuneifolia* was still an indicator for the controls and *S. cryptandrus* was revealed to be an indicator for the seeded-only treatment. A significant treatment effect was found for *D. cuneifolia* ($F = 5.27$, $p = 0.004$) and *S. cryptandrus* ($F = 3.36$, $p = 0.01$). For *D. cuneifolia*, both the controls and seeded-only plots had significantly higher emergence of seedlings than the combined

plots (Fig. 3.4). For *S. cryptandrus*, the seeded-only plots had significantly higher emergence of seedlings than the combined plots.

We also chose to run separate analyses on other species that were abundant in at least one of the post-treatment years. These included *L. humistratus*, *L. denticulatus*, *L. serriola* and *E. cicutarium*. There was no significant treatment effect on *L. humistratus* or *L. serriola* in either 2007 or 2008. A significant difference did exist in 2008 for *L. denticulatus* with herbicide-only plots having more individuals than the controls and the combined plots having more individuals than the seeded-only plots ($F = 3.04$, $p = 0.036$) (Fig. 3.5). Significance was also found in 2008 for *E. cicutarium* with the controls and seeded-only plots having significantly more individuals than the herbicide-only plots ($F = 2.87$, $p = 0.019$) (Fig 3.6).

Description of Soil Seed Bank Community

A total of 7,912 seedlings emerged from the soil samples from 2006-2008 representing 40 species from 25 different families (Tables 3.3, 3.4). The total 3-year community was comprised of 58% annuals, 35% perennials and 7% biennials. A similar proportion was evident for each individual year. Of all the species, 32 (80%) were forbs, 4 (10%) were grasses and 4 (10%) were shrubs. There were 6 nonnative species (15%) present including *Amaranthus albus* (prostrate pigweed), *E. cicutarium*, *Bassia prostrata* (forage kochia), *L. serriola*, *C. testiculata* and *T. ramosissima*. All species detected in the soil seed bank were also in the aboveground community with the exception of *Draba asprella* (rough draba), *Epilobium ciliatum* (fringed willowherb), *T. ramosissima* and *Typha sp.* (cattail) (Table 3.5). In 2006 and 2007, *D. cuneifolia* was the most abundant

and most frequently occurring species. This switched to *V. octoflora* in 2008. Other species commonly encountered during the study were; *E. cicutarium*, *L. denticulatus*, *L. humistratus*, *Conyza canadensis* (Canadian horseweed) and *S. antirrhina*. Of these species, all increased from the first year (3 months post-fire) with the exception of *C. canadensis*. It should also be noted that in 2008, several species declined across all treatments. These include *D. cuneifolia*, *L. humistratus*, *S. antirrhina* and *Myosurus cupulatus* (Arizona mousetail) (Tables 3.2, 3.4).

Discussion

Treatment Effects on the Soil Seed Bank Community

Overall, the treatments did not appear to have much of an effect on the soil seed bank community. We did not expect to see significant within or between plot differences in the first year of the study partly because the treatments had not yet been applied and because seed reserves had yet to be replenished following the fire. However, we had predicted that unique communities would begin to develop following treatment application in the subsequent two years. In chapter two, we found that imazapic was effective at reducing the emergence of annual bromes. Imazapic targets fast growing tissues which makes it ideal for controlling these species based on their tendency to emerge prior to most native, perennial species. However, the soil seed bank community at the study site also contains numerous annual species that share similar growth patterns. We believed that imazapic had the potential to reduce these annual species in addition to the target brome species. At the community level, we did not find this to be the case, at least in terms of statistical significance. We were however able to

detect some general patterns. For example, all indicator species were indicators for unsprayed plots, meaning that they were both more abundant and occurred with greater frequency in these plots as compared to sprayed plots. Similarly, ordination of the plots in 2007, showed a degree of spatial separation in the data based upon whether plots had been sprayed or left unsprayed. This was not true for 2008, but it is quite probable that the herbicide was no longer active at this time. Imazapic can persist in the soil for up to two years on vegetation-depauperate sites, but is commonly metabolized by plants within the first growing season following application (Tu et al. 2001; Davidson and Smith 2007; Matchett et al. 2009).

Analysis of the community based upon life history, growth form and nativity did not produce significant results except when analyzing forbs in 2007 and perennial species in 2008. In 2007, the results appear to have been driven by several forb species that were once again, far more numerous in unsprayed plots than in sprayed plots. The gain in significance when only analyzing forb species is probably due to the removal of *V. octoflora* from the analysis. This annual grass was the only non-forb species found to be in abundance for all treatment types and likely diluted the results when examining the entire community. The significance found when analyzing only perennial species in 2008 was driven by *S. cryptandrus*. Following treatment application, the other seeded species had only minimal emergence. The greater success of *S. cryptandrus* is probably due to the fact that it is the most proficient at producing large quantities of highly viable seed.

Treatment Effects on Individual Species

Several species including *D. cuneifolia*, *S. cryptandrus* and *E. cicutarium* had significantly more emergence in unsprayed plots as compared to sprayed plots suggesting a susceptibility to imazapic. We could not find specific mention of the effects of imazapic on *D. cuneifolia* in the literature, but we did find records of this herbicide reducing numerous other members of the mustard family (*Brassicaceae*) (Davison and Smith 2007; Mangold and Jacobs 2007; Wilson et al. 2010). We also found literature pertaining to the reductive effects of imazapic on *E. cicutarium* (Eddington 2006; Davison and Smith 2007; Wilson et al. 2010). Control of *E. cicutarium* was not the goal of the herbicide treatment, but as it is an invasive, nonnative species its incidental reduction contributed to the restoration efforts implemented at this site.

A significant difference in emergence also occurred with *L. denticulatus*. With this species however, populations were larger in the sprayed plots. *L. denticulatus* is a legume and belongs to the *Fabaceae* family. Trials in other regions of the country have found certain legumes to be resistant of imazapic (Tu et al. 2001). Observations made by field crews during sampling periods noted that there was more bareground in sprayed plots versus unsprayed plots. If *L. denticulatus* is resistant to imazapic, it is possible that less competition coupled with increased resources in the more open sprayed plots allowed it to become more established at these locations. This scenario has been noted in the past with other species. For instance, *Hypochaeris glabra* (smooth catsear), which is highly tolerant of imazapic, has dramatically increased following an imazapic-induced decline of onsite grass species (Kyser et al. 2007). Although not statistically significant,

increases in *L. serriola* were also seen in the sprayed plots. Like *H. glabra*, *L. serriola* belongs to the aster family (*Asteraceae*). Species in this family, like *Fabaceae*, have also shown a particular resistance to imazapic (Beran et al. 1999; Masters et al. 2001).

Community Data

The high percentage of annual species that we found in the seed bank is typical of many post-disturbance pinyon-juniper woodlands. (Allen et al. 2008; Barney and Frischknecht 1974; Koniak 1983). Compositionally, perennial species did make up of a third of the soil seed bank community, but emergence of all perennial species was low. Many of the perennial species observed in the aboveground community germinate fairly readily, which suggests that their reduced emergence in the greenhouse was due to a lack of viable seed. However, as we noted in Chapter 2, *P. palmeri* germination may have been limited due to cold stratification and this process may have affected other species as well. Other factors could also have interfered with perennial seed germination. For example, *G. sarothrae* is common in the aboveground community, but rarely emerged in the greenhouse. Resprouting was probably not a factor as this shrub is a short-lived perennial that relies mostly on large seed crops for reproduction (Peters et al. 1992). Studies have found that seeds require an after-ripening phase of 4-6 months in order to break dormancy and germination is facilitated by moist soils and fluctuating temperatures (Mayeux and Leotta 1981; Wood et al. 1997). All of these conditions were met to some degree, but it is likely that one factor or a combination of factors were not specific enough to maximize germination. Other species such as *Nicotiana attenuata* (coyote tobacco), *Purshia tridentata* (Antelope bitterbrush) and

Achnatherum hymenoides (Indian ricegrass) germinate more reliably when exposed to smoke (Baldwin et al. 1994; Blank and Young 1998). All of these species are present in the understory, but none emerged from the soil samples in the greenhouse.

The rapid, overall decline noted in several of the annual species is interesting, but not necessarily unusual. In the case of *C. canadensis*, this species is known to be opportunistic following fire, but rarely persists for more than 1-2 years in wildland settings (Crawford et al. 2001; Barclay et al. 2004). The marked decrease across all treatments of *D. cuneifolia*, *L. humistratus*, *S. antirrhina* and *Myosurus cupulatus* (Arizona mousetail) can probably be attributed to much lower precipitation at the beginning of the growing season as compared to 2007. Even if these species had contributed ample seed to the soil seed bank the previous summer, the dry spring conditions of 2008 most likely had a dampening effect on germination. However, other species such as *L. serriola* and *L. denticulatus* were more abundant. We do not know the precise reason for this increase, but it may be related to having more flexibility in germination requirements and having more seed available for germination. Competition probably affected rates of decrease as well. We did not see a significant compositional shift from annual to perennials species in this study, but gains and losses in annual species is a common phenomena in early successional plant communities (Kleiner 1982; Pyke and Archer 1991; Aikio et al. 2002; Korb et al 2005).

Conclusion

In chapter two, occurrence of the targeted *Bromus* species was substantially reduced by imazapic. In this chapter however, we found that dramatic reductions did not extend to the rest of the soil seed bank community. There were significant reductions of several annual forbs, especially *D. cuneifolia* and *E. cicutarium*, in sprayed plots and it is possible that at least two of the perennial seeded species (*S. cryptandrus* and *S. ambigua*) were also reduced due at least in part to the presence of herbicide. Overall though, imazapic/vegetation interactions were mostly limited to the target species. Therefore, at our site, the trade-off between *Bromus* control and unintentional control of native species was at an acceptable level as determined through analysis of the soil seed bank. However, in locations not possessing a great abundance of *Bromus* individuals, the risk of damaging native populations increases and much discretion is warranted when deciding whether or not to apply imazapic.

The increase in non-native species in the last year of the study suggests that further steps need to be taken to insure native establishment during the first year of imazapic application. In this case, implementing a time-lag between spraying and seed application might have been sufficient, but additional research needs to be conducted. Confounding factors such as below-average precipitation and sample preparation could certainly have contributed the negative results reported from this study. The ability of some species to exist at high numbers in sprayed plots is both encouraging and cautionary. Incorporating annual species like *L. denticulatus* may work well in restoration if ways are found to harvest seed in a practical fashion. However, managers

need to be aware that potentially imazapic-resistant, nonnative species may also be able to take advantage of reduced competition and simply replace the original problem. Finally, our study dealt with the soil seed bank and the majority of the data pertained only to annual species. To truly determine the effects of imazapic on the understory component of this study site, the results should be incorporated into the effects of imazapic on the aboveground community as well.

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Table 3.1. Significant indicator species for the soil seed bank community for 2007 and 2008. To be significant, species had to have an Indicator Value of ≥ 25 and a p value ≤ 0.05 .

Species	Year					
	2007			2008		
	Group ¹	IV ²	p value ³	Group ¹	IV ²	p value ³
<i>Cryptantha gracilis</i>	control	32.1	0.0335	-	-	-
<i>Draba cuneifolia</i>	control	50.9	0.0190	control	43.8	0.0074
<i>Silene antirrhina</i>	control	48.0	0.0267	-	-	-
<i>Sporobolus cryptandrus</i>	-	-	-	seeded	36.5	0.0201

¹Represents the treatment type for which the species was a significant indicator species.

²IV = Indicator Value. Indicator values are the percent of perfect indication, based on combining the values for relative abundance and relative frequency

³P-values represent the proportion of randomized trials with indicator value equal to or exceeding the observed indicator value.

Table 3.2. Summary of species characteristics and number of seedlings emerging from soil samples following application of treatments.

Species	Life Form ¹	2007				2008			
		Treatment ²				Treatment ²			
		C	S	H	CD	C	S	H	CD
Annual									
<i>Amaranthus albus</i> *	F	0	0	1	0	2	0	0	0
<i>Astragalus nuttallianus</i>	F	0	0	1	5	0	0	1	1
<i>Ceratocephala testiculata</i> *	F	1	20	1	2	0	9	2	0
<i>Claytonia perfoliata</i>	F	0	0	1	0	0	0	0	0
<i>Conyza canadensis</i>	F	5	3	1	1	6	3	9	1
<i>Cryptantha gracilis</i>	F	18	4	3	3	2	1	0	0
<i>Draba cuneifolia</i>	F	594	315	112	147	184	123	69	44
<i>Eriogonum palmeranum</i>	F	0	1	2	3	2	0	0	0
<i>Erodium cicutarium</i> *	F	100	62	31	38	99	121	22	30
<i>Gilia inconspicua</i>	F	4	2	1	7	3	2	3	2
<i>Lotus denticulatus</i>	F	5	5	22	6	24	15	109	74
<i>Lotus humistratus</i>	F	64	50	65	109	26	19	39	57
<i>Lupinus kingii</i>	F	0	0	0	0	0	1	1	0
<i>Microseris lindleyi</i>	F	1	0	1	0	0	0	2	0
<i>Mimulus rubellus</i>	F	0	0	0	0	0	1	0	0
<i>Myosurus cupulatus</i>	F	20	7	14	13	2	2	5	1
<i>Phacelia fremontii</i>	F	0	0	0	0	0	1	0	0

<i>Plantago patagonica</i>	F	51	28	38	5	9	9	13	2
<i>Silene antirrhina</i>	F	147	82	24	155	45	56	21	3
<i>Vicia ludoviciana</i>	F	0	2	2	0	0	0	0	0
<i>Vulpia octoflora</i>	G	351	338	193	110	173	186	431	67
Biennial									
<i>Cirsium neomexicanum</i>	F	0	0	0	1	0	0	0	0
<i>Descurainia pinnata</i>	F	11	30	9	5	5	2	2	1
<i>Lactuca serriola</i> *	F	10	3	9	8	83	22	151	110
Perennial									
<i>Chamaesyce albomarginata</i>	F	5	2	2	2	0	1	1	4
<i>Cylindropuntia whipplei</i>	S	1	0	0	0	0	3	1	0
<i>Elymus elymoides</i> **	G	1	7	0	1	2	0	2	0
<i>Gutierrezia sarothrae</i>	S	0	0	1	4	0	1	2	2
<i>Penstemon palmeri</i> **	F	1	6	0	3	2	0	0	0
<i>Poa secunda</i>	G	5	5	3	9	0	0	0	1
<i>Sphaeralcea ambigua</i> **	F	0	0	1	0	2	3	1	0
<i>Sporobolus cryptandrus</i> **	G	1	1	0	0	5	64	2	2
<i>Tamarix ramosissima</i> *	S	0	0	1	0	0	0	0	0
Total		1,396	973	539	637	676	645	889	402
Seeds/m²		25,579	17,378	10,457	12,229	12,984	11,520	17,270	7,484
# Species		22	21	25	20	19	21	19	16

*nonnative species

**seeded species

¹Life Form: F = forb, G = grass, S = shrub

²Treatment: C = control, S = seeded, H = herbicide, CD = combined

Table 3.3. Summary of species as arranged by family.

Family	Family
Amaranthaceae	Hydrophyllaceae
<i>Amaranthus albus</i>	<i>Phacelia fremontii</i>
Asteraceae	Malvaceae
<i>Cirsium neomexicanum</i>	<i>Sphaeralcea ambigua</i>
<i>Conyza canadensis</i>	Onagraceae
<i>Gutierrezia sarothrae</i>	<i>Epilobium ciliatum</i>
<i>Lactuca serriola</i>	Plantaginaceae
<i>Microseris lindleyi</i>	<i>Plantago patagonica</i>
Boraginaceae	Poaceae
<i>Cryptantha gracilis</i>	<i>Bromus rubens</i>
Brassicaceae	<i>Bromus tectorum</i>
<i>Descurainia pinnata</i>	<i>Elymus elymoides</i>
<i>Draba asprella</i> var. <i>zionensis</i>	<i>Poa secunda</i>
<i>Draba cuneifolia</i>	<i>Sporobolus cryptandrus</i>
Cactaceae	<i>Vulpia octoflora</i>
<i>Cylindropuntia whipplei</i>	Polemoniaceae
Caryophyllaceae	<i>Eriastrum diffusum</i>
<i>Silene antirrhina</i>	<i>Gilia inconspicua</i>
Chenopodiaceae	Polygonaceae
<i>Kochia prostrata</i>	<i>Eriogonum palmerianum</i>
Euphorbiaceae	Portulacaceae
<i>Chamaesyce albomarginata</i>	<i>Claytonia perfoliata</i>
Fabaceae	Ranunculaceae
<i>Astragalus nuttallianus</i>	<i>Ceratocephala testiculata</i>
<i>Lotus denticulatus</i>	<i>Myosurus cupulatus</i>
<i>Lotus humistratus</i>	Rosaceae
<i>Lupinus kingii</i>	<i>Purshia stansburiana</i>
<i>Vicia ludoviciana</i>	
Gentianaceae	
<i>Centaurium calycosum</i>	
Geraniaceae	
<i>Erodium cicutarium</i>	

Table 3.4. List of all species and total number of emerged seedlings for all years of the study.

Species	Year		
	2006	2007	2008
<i>Amaranthus albus</i>	-	1	2
<i>Astragalus nuttallianus</i>	2	6	2
<i>Centaureum calycosum</i>	1	-	-
<i>Ceratocephala testiculata</i>	7	24	11
<i>Chamaesyce albomarginata</i>	1	11	6
<i>Conyza canadensis</i>	184	10	19
<i>Cryptantha gracilis</i>	4	28	3
<i>Cylindropuntia whipplei</i>	3	1	4
<i>Cirsium neomexicanum</i>	-	1	-
<i>Descurainia pinnata</i>	4	55	10
<i>Draba asprella</i>	92	-	-
<i>Claytonia perfoliata</i>	-	1	-
<i>Draba cuneifolia</i>	599	1,168	420
<i>Epilobium ciliatum</i>	2	-	-
<i>Eriastrum diffusum</i>	1	-	-
<i>Elymus elymoides</i>	-	9	4
<i>Eriogonum palmerianum</i>	-	6	2
<i>Erodium cicutarium</i>	91	231	272
<i>Gilia inconspicua</i>	2	14	10
<i>Gutierrezia sarothrae</i>	1	5	5
<i>Kochia prostrata</i>	2	-	-
<i>Lactuca serriola</i>	4	30	366
<i>Lotus denticulatus</i>	38	38	222
<i>Lotus humistratus</i>	101	288	141
<i>Lupinus kingii</i>	-	-	2
<i>Microseris lindleyi</i>	-	2	2
<i>Mimulus rubellus</i>	-	-	1
<i>Myosurus cupulatus</i>	50	54	10
<i>Penstemon palmeri</i>	-	10	2
<i>Phacelia fremontii</i>	1	-	1
<i>Plantago patagonica</i>	14	122	33
<i>Poa secunda</i>	14	22	1
<i>Purshia mexicana</i>	2	-	-
<i>Silene antirrhina</i>	229	408	125
<i>Sphaeralcea ambigua</i>	-	1	6
<i>Sporobolus cryptandrus</i>	-	2	73
<i>Tamarix ramosissima</i>	-	1	-
<i>Typha sp.</i>	1	-	-

<i>Vicia ludoviciana</i>	-	4	-
<i>Vulpia octoflora</i>	305	992	857
Total	1,755	3,535	2,610
Seeds/m2	31,344.30	65,641.16	49,257.11
# Species	27	29	28

Table 3.5. Summary of species in the aboveground community. Species also found in the soil seed bank are marked with an **X** in the columns labeled SB.

SB	Aboveground	SB	Aboveground	SB	Aboveground	SB	Aboveground	SB	Aboveground
	<i>Abronia fragrans</i>		<i>Chaenactis stevioides</i>		<i>Eriodictyon angustifolium</i>		<i>Marrubium vulgare</i>		<i>Polygonum aviculare</i>
	<i>Achnatherum hymenoides</i>		<i>Chaetopappa ericoides</i>		<i>Eriogonum davidsonii</i>		<i>Medicago sativa</i>		<i>Portulaca oleracea</i>
	<i>Achnatherum speciosum</i>	X	<i>Chamaesyce albomarginata</i>		<i>Eriogonum fasciculatum</i>		<i>Melica bulbosa</i>		<i>Pseudognaphalium canescens</i>
	<i>Acourtia wrightii</i>		<i>Chamaesyce fendleri</i>		<i>Eriogonum inflatum</i>		<i>Melilotus officinalis</i>		<i>Psoralea argemone</i>
	<i>Agropyron cristatum</i>		<i>Chamaesyce glyptosperma</i>		<i>Eriogonum microthecum</i>		<i>Mentzelia albicaulis</i>	X	<i>Purshia stansburiana</i>
	<i>Aliciella leptomeria</i>		<i>Chenopodium album</i>	X	<i>Eriogonum palmerianum</i>		<i>Mentzelia multiflora</i>		<i>Purshia tridentata</i>
	<i>Allium bisceptrum</i>		<i>Chenopodium fremontii</i>		<i>Eriogonum umbellatum</i>	X	<i>Microseris lindleyi</i>		<i>Quercus turbinella</i>
X	<i>Amaranthus albus</i>		<i>Chrysothamnus viscidiflorus</i>	X	<i>Erodium cicutarium</i>		<i>Microsteris gracilis</i>	X	<i>Ranunculus testiculata</i>
	<i>Amaranthus blitoides</i>	X	<i>Cirsium neomexicanum</i>		<i>Erysimum capitatum</i>	X	<i>Mimulus rubellus</i>		<i>Rhus trilobata</i>
	<i>Ambrosia acanthicarpa</i>	X	<i>Claytonia perfoliata</i>		<i>Erysimum repandum</i>		<i>Mirabilis linearis</i>		<i>Rhus trilobata</i>
	<i>Amelanchier alnifolia</i>		<i>Comandra umbellata</i>		<i>Eucrypta micrantha</i>		<i>Mirabilis multiflora</i>		<i>Rumex hymenosepalus</i>
	<i>Amelanchier utahensis</i>		<i>Conringia orientalis</i>		<i>Eurybia glauca</i>		<i>Mollugo cerviana</i>		<i>Salsola tragus</i>
	<i>Anemone tuberosa</i>		<i>Convolvulus arvensis</i>		<i>Fraxina albomarginata</i>		<i>Muhlenbergia asperifolia</i>		<i>Salvia dorrii</i>
	<i>Antheropeas wallacei</i>	X	<i>Conyza canadensis</i>		<i>Fraxinus anomala</i>		<i>Muhlenbergia porteri</i>		<i>Schizachyrium scoparium</i>
	<i>Arabis holboellii</i>		<i>Cordylanthus parviflorus</i>		<i>Gaillardia pinnatifida</i>		<i>Myosurus cupulatus</i>		<i>Shepherdia rotundifolia</i>
	<i>Arctostaphylos pungens</i>		<i>Corydalis aurea</i>	X	<i>Gilia inconspicua</i>		<i>Nicotiana attenuata</i>	X	<i>Silene antirrhina</i>
	<i>Arenaria macradenia</i>		<i>Crepis occidentalis</i>		<i>Gilia sinuata</i>		<i>Oenothera albicaulis</i>		<i>Sisymbrium altissimum</i>
	<i>Argemone munita</i>		<i>Cryptantha ambigua</i>		<i>Grindelia squarrosa</i>		<i>Oenothera caespitosa</i>		<i>Solanum triflorum</i>
	<i>Aristida purpurea</i>		<i>Cryptantha barbigera</i>	X	<i>Gutierrezia sarothrae</i>		<i>Oenothera pallid</i>		<i>Solidago velutina</i>
	<i>Artemisia filifolia</i>		<i>Cryptantha circumscissa</i>		<i>Helianthus annuus</i>		<i>Opuntia basilaris</i>		<i>Sonchus oleraceus</i>
	<i>Artemisia ludoviciana</i>		<i>Cryptantha confertiflora</i>		<i>Hesperostipa comata</i>		<i>Opuntia engelmannii</i>		<i>Sorghum bicolor</i>
	<i>Artemisia tridentata</i>	X	<i>Cryptantha gracilis</i>		<i>Heterotheca villosa</i>		<i>Opuntia phaeacantha</i>	X	<i>Sphaeralcea ambigua</i>
	<i>Asclepias asperula</i>		<i>Cryptantha micrantha</i>		<i>Hordeum murinum</i>		<i>Packera multilobata</i>		<i>Sphaeralcea grossulariifolia</i>
	<i>Asclepias subverticillata</i>		<i>Cryptantha pterocarya</i>		<i>Hymenopappus filifolius</i>		<i>Parietaria pensylvanica</i>		<i>Sporobolus contractus</i>
	<i>Astragalus amphioxys</i>		<i>Cryptantha virginensis</i>		<i>Hymenoxys cooperi</i>		<i>Pasopyrum smithii</i>	X	<i>Sporobolus cryptandrus</i>
	<i>Astragalus zionis</i>	X	<i>Cylindropuntia whipplei</i>		<i>Ipomopsis aggregata</i>		<i>Pectis papposa</i>		<i>Stanleya pinnata</i>
X	<i>Astragalus nuttallianus</i>		<i>Cymopterus multinervatus</i>		<i>Juniperus osteosperma</i>		<i>Pectocarya setosa</i>		<i>Stephanomeria exigua</i>
	<i>Atriplex canescens</i>		<i>Cymopterus purpureus</i>	X	<i>Kochia prostrata</i>		<i>Pediomelum mephiticum</i>		<i>Stephanomeria pauciflora</i>
	<i>Avena fatua</i>		<i>Dalea searsiae</i>	X	<i>Lactuca serriola</i>		<i>Pellaea truncate</i>		<i>Streptanthella longirostris</i>

<i>Baileya multiradiata</i>		<i>Dasyochloa pulchella</i>		<i>Lactuca tatarica</i>		<i>Penstemon eatonii</i>		<i>Streptanthus cordatus</i>
<i>Bassia scoparia</i>		<i>Datura wrightii</i>		<i>Langloisia setosissima</i>		<i>Penstemon pachyphyllus</i>		<i>Symphoricarpos longiflorus</i>
<i>Bouteloua barbata</i>		<i>Delphinium scaposum</i>		<i>Lappula occidentalis</i>	X	<i>Penstemon palmeri</i>		<i>Thysanocarpus curvipes</i>
<i>Bouteloua eriopoda</i>	X	<i>Descurainia pinnata</i>		<i>Layia glandulosa</i>		<i>Penstemon utahensis</i>		<i>Townsendia incana</i>
<i>Bouteloua gracilis</i>		<i>Descurainia sophia</i>		<i>Lepidium fremontii</i>		<i>Pentagramma triangularis</i>		<i>Tradescantia occidentalis</i>
<i>Brickellia atractyloides</i>		<i>Dichelostemma capitatum</i>		<i>Lepidium lasiocarpum</i>		<i>Peteria thompsoniae</i>		<i>Tragia ramosa</i>
<i>Brickellia californica</i>	X	<i>Draba cuneifolia</i>		<i>Lepidium virginicum</i>		<i>Phacelia cryptantha</i>		<i>Tragopogon dubius</i>
<i>Bromus berterianus</i>		<i>Echinocereus engelmannii</i>		<i>Linanthus dichotomus</i>		<i>Phacelia curvipes</i>		<i>Tribulus terrestris</i>
<i>Bromus diandrus</i>		<i>Echinocereus triglochidiatus</i>		<i>Linum lewisii</i>	X	<i>Phacelia fremontii</i>		<i>Verbena bracteata</i>
<i>Bromus inermis</i>		<i>Elymus canadensis</i>		<i>Logfia californica</i>		<i>Phacelia ivesiana</i>	X	<i>Vicia ludoviciana</i>
X <i>Bromus rubens</i>	X	<i>Elymus elymoides</i>	X	<i>Lotus denticulatus</i>		<i>Phacelia vallis-mortae</i>	X	<i>Vulpia octoflora</i>
X <i>Bromus tectorum</i>		<i>Encelia virginensis</i>	X	<i>Lotus humistratus</i>		<i>Phlox austromontana</i>		<i>Xanthium strumarium</i>
<i>Calochortus flexuosus</i>		<i>Ephedra nevadensis</i>		<i>Lotus plebeius</i>		<i>Phlox longifolia</i>		<i>Yucca baccata</i>
<i>Calochortus nuttallii</i>		<i>Ephedra torreyana</i>		<i>Lotus rigidus</i>		<i>Physalis hederifolia</i>		<i>Zigadenus paniculatus</i>
<i>Camissonia brevipes</i>		<i>Ephedra viridis</i>	X	<i>Lupinus kingii</i>		<i>Pinus monophylla</i>		
<i>Camissonia multijuga</i>		<i>Eragrostis cilianensis</i>		<i>Lupinus latifolius</i>	X	<i>Plantago patagonica</i>		
<i>Camissonia parvula</i>	X	<i>Eriastrum diffusum</i>		<i>Lupinus pusillus</i>		<i>Pleuraphis jamesii</i>		
<i>Castilleja angustifolia</i>		<i>Eriastrum eremicum</i>		<i>Lycium pallidum</i>		<i>Pleuraphis rigida</i>		
<i>Castilleja linariifolia</i>		<i>Ericameria linearifolia</i>		<i>Machaeranthera</i>		<i>Poa bigelovii</i>		
X <i>Centaurium calycosum</i>		<i>Erigeron concinnus</i>		<i>Machaeranthera gracilis</i>		<i>Poa bulbosa</i>		
<i>Centrostegia thurberi</i>		<i>Erigeron divergens</i>		<i>Machaeranthera</i>		<i>Poa fendleriana</i>		
<i>Chaenactis douglasii</i>		<i>Erigeron utahensis</i>		<i>Malcolmia africana</i>	X	<i>Poa secunda</i>		

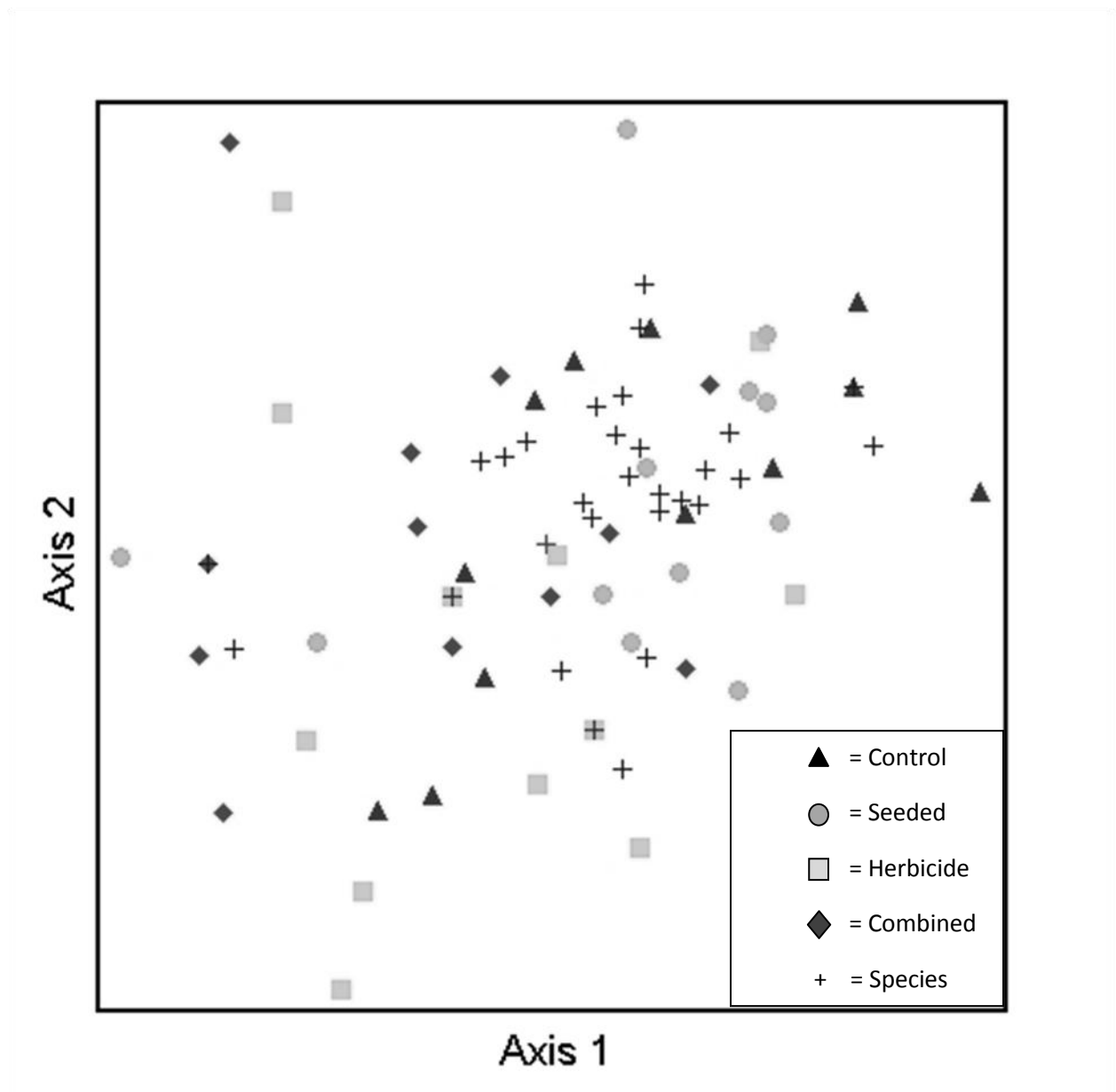


Figure 3.1. Non-metric multi-dimensional scaling (NMS) plot of soil seed bank communities in 2007. Individual symbols represent individual plots. This configuration was determined using the abundance of 30 species on 48 plots. The final solution had two dimensions with a final stress of 17.80.

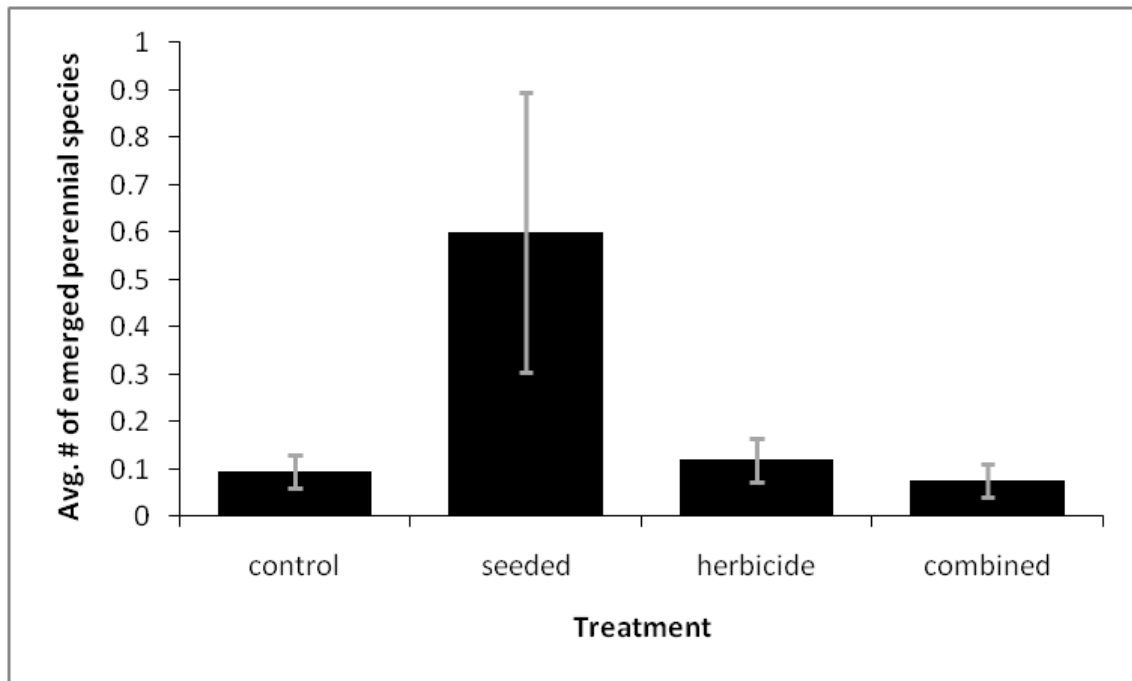


Figure 3.2. Comparison of average number of perennial species emerged from soil samples, by treatment, for 2008 with standard error bars.

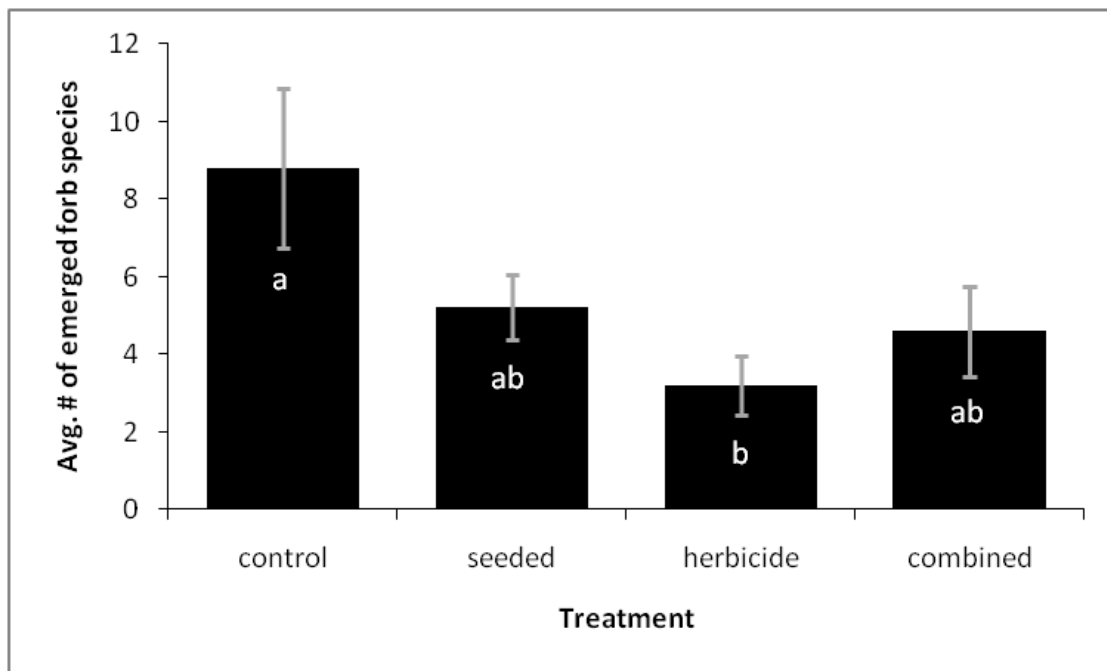


Figure 3.3. Comparison of average number of forb species emerged from soil samples, by treatment, for 2007 with standard error bars. Means sharing a letter do not differ at $p < 0.05$.

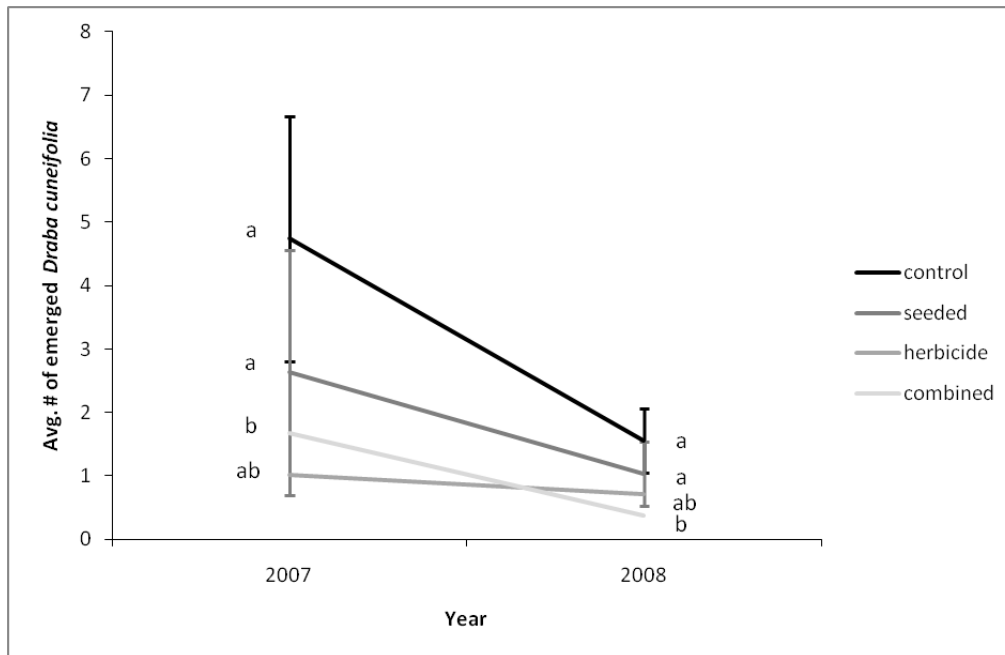


Figure 3.4. Comparison of average number of *Draba cuneifolia* emerged, by treatment, for 2007 and 2008 with standard error bars. Means sharing a letter do not differ at $p < 0.05$. Letters indicate only within year differences, not between year differences.

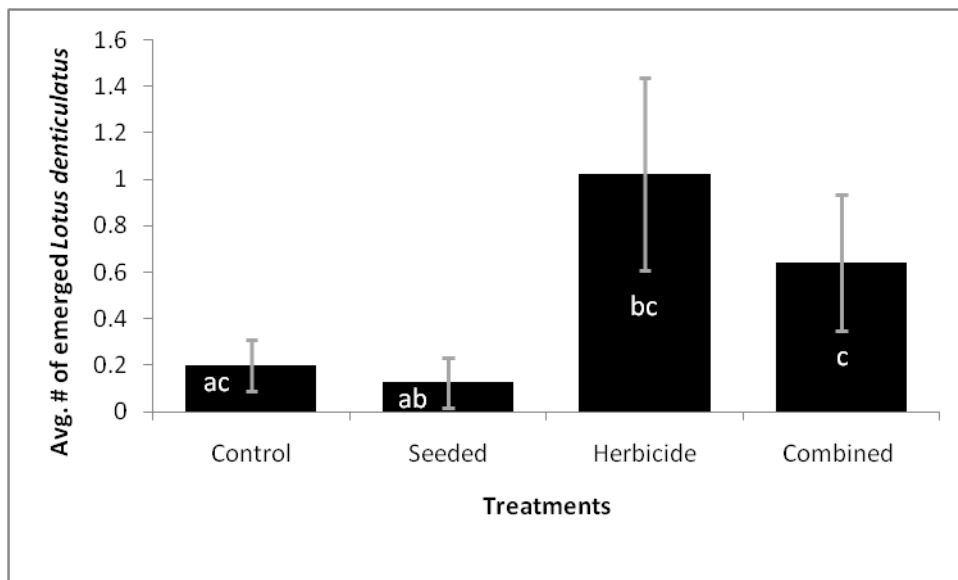


Figure 3.5. Comparison of average number of *Lotus denticulatus* emerged from soil samples, by treatment, for 2008 with standard error bars. Means sharing a letter do not differ at $p < 0.05$.

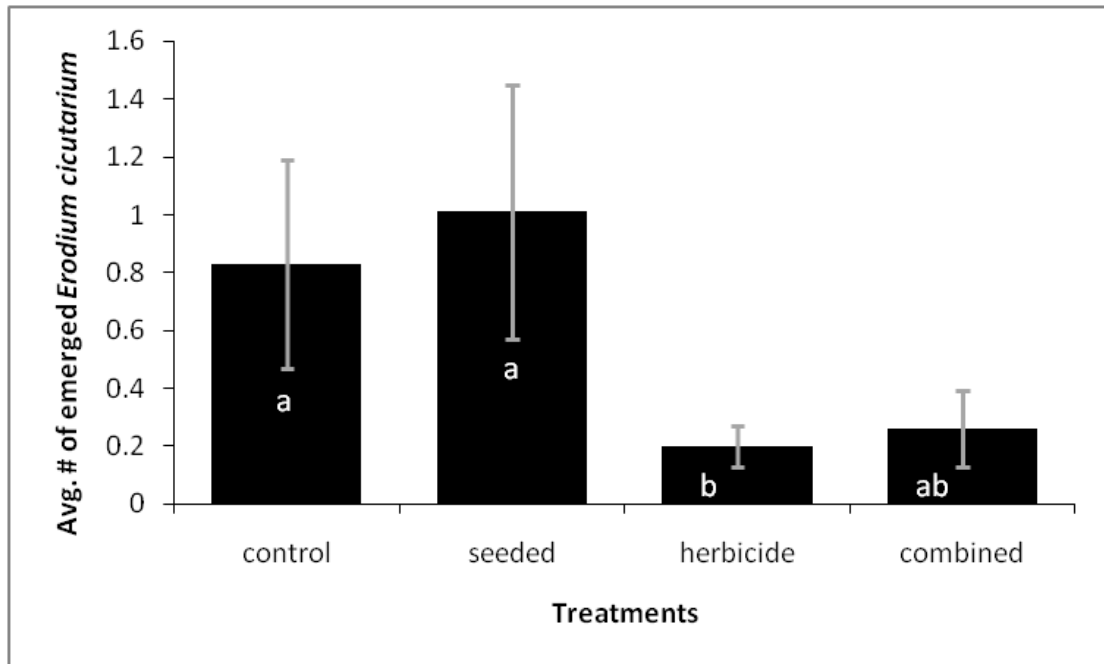


Figure 3.6. Comparison of average number of *Erodium cicutarium* emerged from soil samples, by treatment, for 2008 with standard error bars. Means sharing a letter do not differ at $p < 0.05$.

CHAPTER 4

Management Implications

This study is one of the few that has monitored the effects of imazapic and native seeding on a soil seed bank community and the only one that we know of that has done so in a pinyon-juniper woodland. The reduction of the target brome species for one year is similar to the findings of other studies examining the efficacy of imazapic on reducing invasive annuals in aboveground plant communities (Bekedam 2005; Vollmer and Vollmer 2006; Kyser et al. 2007; Baker et al. 2009). We also found that some non-target species were reduced, but overall, the effect on the entire soil seed bank community was not significant. Our results suggest, but do not confirm that imazapic may have had an adverse effect on the emergence of at least two of the seeded, native species (*S. cryptandrus* and *S. ambigua*). In general, the seeded, native species made only a minimal contribution to the soil seed bank and had little effect on reducing *Bromus* species. However, the increase in *S. cryptandrus* during the last year of study suggests, that it may become a more substantial component of the seed bank in the next few years.

Although the herbicide treatment did not have a significant impact on the community present at the study site, our results on individual species and the results of other studies implies that inadvertent control of native species is a reality. Therefore, prudence is recommended when deciding if imazapic is the correct choice for achieving management goals. There still remains a need for finding better ways to restore *Bromus*

dominated systems. Use of the herbicide imazapic shows promise, but further research needs to be conducted both on the susceptibility of native species in general and on the timing of seeding additions in relation to imazapic applications. Finding site-adapted natives that can quickly replenish fire-impooverished seed banks would also be beneficial. This study and others indicate that *S. cryptandrus* may be able to fulfill this role in areas where it naturally grows. Also, the increase in non-native species in the last year of the study suggests that further steps need to be taken to insure native establishment during the first year of imazapic application.

Finally, results from this study advocate for the inclusion of seed bank assays in guiding management decisions and monitoring restoration actions. Examination of the soil seed bank following treatments strengthened the results produced by the co-occurring aboveground study (Thode et al. 2010). Data collected from the soil seed bank would be useful in deciding whether or not additional measures, such as herbicide application, should be taken to advance recovery in disturbed areas. If a disturbance (i.e. thinning, prescribed fire) is planned for an area, this same knowledge would provide managers insight on what to expect regarding the release of non-natives following such an action. The close correlation between summer seed crops and *Bromus* species emergence could allow seed bank assays to supplant aboveground assessments. Access to a greenhouse facility would be necessary, but field collections would require less time and personnel and soils can be stored for several years with little effect on seed viability (Hulbert 1955).

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